Improving representations of higher trophic-level species in models: Using individual-based modelling and dynamic energy budget theory to project population trajectories of southern elephant seals

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Statements and Declarations

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This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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Chapter 3: Authors 1 and 2 provided advice during initial model development. Authors 1, 2, 3 and 5 provided technical advice on model development and approaches to the sensitivity analyses. Author 2 provided advice on statistical analyses. Author 1 provided in depth discussion on mathematics in the model. All contributing authors provided comments on the manuscript.
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Statement of Ethical Conduct

The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University. The study was carried out at Macquarie Island under ethics approval from the Australian Antarctic Animal Ethics Committee (AAS 2265 and AAS 2794) and the Tasmanian Parks and Wildlife Service.

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I don't know where I'm going from here,
but I promise it won't be boring.

DAVID BOWIE

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Abstract

Higher trophic-level marine predators are of particular interest to ecologists, as these species can be used to observe direct and indirect effects of changes to ecosystem dynamics and physical environments. The population dynamics of these species and their breeding and foraging traits can inform ecosystem-based fisheries management, such as that which has been adopted by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) for the Southern Ocean.

This thesis presents and applies a framework for representing marine mammals in ecosystem models, using dynamic energy budget (DEB) theory incorporated in individual-based models (IBMs). It investigates effects at a population level while taking into account individual traits, as well as energetic requirements of the selected species. The model is the first of its kind for a large marine mammal.

Chapter 1 justifies the selection of the southern elephant seal *Mirounga leonina* as the study species, for which good demographic data are available, and summarises the thesis approach. Chapter 2 discusses how detailed representations of apex (non-fish) predators are generally lacking from ecosystem models. This is likely due to the challenges involved in representing complex life histories (*i.e.* capital or income breeders, intermittent reproduction, site fidelity) of mammals and birds in ecosystem models. This chapter uses a nested qualitative network model to show that the level of detail with which higher trophic-level species are represented in ecosystem models can have implications for ecosystem-level predictions.

Chapter 3 develops a DEB-IBM for southern elephant seals, using data from longitudinal studies from Macquarie Island. This model i) simulates energy use and life histories, as well as breeding traits in an emergent manner, ii) projects a stable population over time, and iii) has realistic population dynamics and structure based on emergent life history features. Chapter 4 investigates whether the DEB-IBM can assist in evaluating hypotheses regarding drivers of the decline of the southern elephant seal population on Macquarie Island. Results from this chapter suggest a number of interacting drivers for population decline. Finally, Chapter 5 discusses and addresses limitations of the model. It discusses future versions of the model that could be made spatially explicit; include males; be adjusted for other species; and be incorporated in end-to-end ecosystem models to improve higher trophic level species representations.

Chapter 1

Context of the thesis

1.1 Introduction

Climate change impacts on ecosystems have been increasing in recent years, at local and global scales, affecting biological, ecological and social systems (Parmesan and Yohe, 2003; IPCC, 2007; Constable et al., 2014). Marine ecosystems are, for example, affected by increases in temperature driving coral bleaching and mortality in the tropics, and changes in sea-ice extent at the poles (Hoegh-Guldberg and Bruno, 2010; Constable et al., 2014). Such changes highlight the need to be able to assess ecosystem status and trends for decision-making in management of marine environments (Constable, 2011; Melbourne-Thomas et al., 2017). This can be achieved through a combination of observations, and statistical and dynamical models.

It is important to be able to detect and attribute the causes of change in predator populations. Predators are important in ecosystems considering the many major roles they play in stabilising ecosystems through top-down forcing, predation (Estes et al., 2011) and by making ecosystems more resistant to stress; providing insurance against climate change impacts on ecosystems (Sala, 2006). Predators in the Southern Ocean are of particular interest due to likely changes to the physical environment (Constable et al., 2014) and significant changes in ecosystem dynamics due to the ongoing recovery of whale and seal populations after their historic near extinction in the 18th to 20th centuries (Croxall et al., 1992; Trivelpiece et al., 2011; Murphy et al., 2012; Constable et al., 2014). Considering the abundant predator populations in the region that rely on krill and fish as a significant proportion of their diets (*e.g.* Hindell et al., 2011; Bedford et al., 2015), and the increase in the size of the commercial Antarctic krill fishery (Trathan et al., 2007; Nicol et al., 2012; Constable et al.,

2014) there is considerable impetus for ecosystem research and model development for the Southern Ocean.

Ecosystem models allow future projections to be made, and can extrapolate from incomplete data. These models can help us understand the effects of change to ecosystems, populations, and individuals, by testing hypotheses using a wide range of scenarios (*e.g.* Forrest et al., 2015; Bodin et al., 2017). In the Southern Ocean the need for assessing ecosystem status and trends is embedded in the ecosystem approach to fisheries management of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Management of marine ecosystems and fisheries uses a range of models, including single- and multi-species and population models, with modelling scopes and frameworks ranging from simple to extremely complex, and from physical, to ecological, to end-to-end ecosystem models which combine physical, chemical, biological and human (social) systems (*e.g.* Fulton et al., 2003; Murphy et al., 2012; Melbourne-Thomas et al., 2017, and references therein).

Changes in populations of higher trophic level predators can indicate direct and indirect effects of perturbation to ecosystem dynamics. Data collected through observations and tracking of these populations add value to models that inform ecosystem based (fisheries) management (see *e.g.* CCAMLR). The tracking data can be used to show foraging ranges and behaviour of species, which can highlight high-priority foraging areas as well as differences in foraging behaviour throughout the year (*e.g.* O'Toole et al., 2015; Hindell et al., 2017); inclusion of this information may be crucial to model developments, especially in regards to ecosystem based (fisheries) management (*e.g.* Horne et al., 2010; Murphy et al., 2012; Essington and Plagányi, 2014). The Southern Ocean is a good region to use for the development of these ecosystem models as there is valuable data available for predator species (see longitudinal studies by McMahon et al., 2005b; Emmerson and Southwell, 2011; Hindell et al., 2017), there is space to improve models, and the developed models will get used by CCAMLR.

The dietary requirements and energetics of predators are important components to understanding predator populations and ecosystem dynamics (*e.g.* Southwell et al., 2015; McHuron et al., 2018). Bioenergetics models have been used for food consumption estimates and fisheries management and research, although none include the energetics of higher trophic-level species such as marine mammals or seabirds, in combination with their foraging behaviour, breeding and population dynamics (Fulton et al., 2003; Gray et al., 2006; Fiechter et al., 2016; Goedegebuure et al., 2017). Part of the reason these models have not yet been developed is due to the uncertainty in model parameters (Chipps and Wahl, 2008), and because higher trophic-level (non-fish) predators of the Southern Ocean have complex life histories

(see Table 2.1). Some of these traits include delayed and intermittent reproduction, complex breeding behaviours and foraging behaviours in complex three-dimensional prey fields.

In general, the parameterisation of bioenergetics models is important, yet difficult to quantify, thus other methods need to be developed. The objective of this project is to find a method which allows for parameterisation of bioenergetics of higher trophic level species that can be included in individual-based models (IBMs; Grimm et al., 2005; Railsback and Grimm, 2011; Grimm et al., 2017). Sibly et al. (2013) reviewed the inclusions of energy budgets in IBMs for animal populations. They discuss different methods for energetics inclusion in models, such as the metabolic theory of ecology (MTE) (Brown et al., 2004), ontogenetic growth model (West et al., 2001) and dynamic energy budget theory (DEB) (Kooijman, 2010b). While the focus of such modelling techniques lies predominantly with fish species, we see the more flexible nature of DEB theory as an effective tool for the development of a model that uses energetics as well as behavioural and breeding traits of higher trophic level species.

Dynamic energy budget (DEB) theory (Kooijman, 2010b) uses a balanced approach for mass and energy to understand the dynamics of biological systems. It considers the assimilation and energy use of an individual organism for growth, maintenance and reproduction (Kooijman, 2010b; Sousa et al., 2010; Martin et al., 2012; Goedegebuure et al., 2018). Recent advances in modelling approaches, such as the development of 'DEBtool' (http://www.debtheory.org/) which can estimate energetics parameters for any species (Chapter 3) without requiring to fill all parameters with observational data, enables the development of complex population models that take individual behaviour and energetic requirements into account.

Combining DEB theory and IMBs allows investigation on how changes at an individual level can produce a population response in a DEB-IBM framework (Martin et al., 2012; Goedegebuure et al., 2017). This framework has previously been used to model water-fleas *Daphina magna* (Martin et al., 2012, 2013); Antarctic krill *Euphausia superba* (Groeneveld et al., 2015); anchovies *Engraulis encrasicolus* (Pethybridge et al., 2013); and recently for the Australian sleepy lizard *Tiliqua rugosa* (Malishev et al., 2018). To incorporate bioenergetics, breeding and foraging behaviour into a model that can be used for representing higher trophic-level predators we opted to adapt a DEB-IBM (Martin et al., 2012, 2013, originally developed for water fleas) to the southern elephant seal *Mirounga leonina*; a species for which significant detailed data are available through longitudinal studies (*e.g.* McMahon et al., 2005b; Hindell et al., 2017). We have used DEBtool to fill the gaps in the southern elephant seal energetics and used life-history data from Macquarie Island for the IBM components of the model. The DEB-IBM modelling environment for southern elephant seals is visually explained in Figure

1.1.

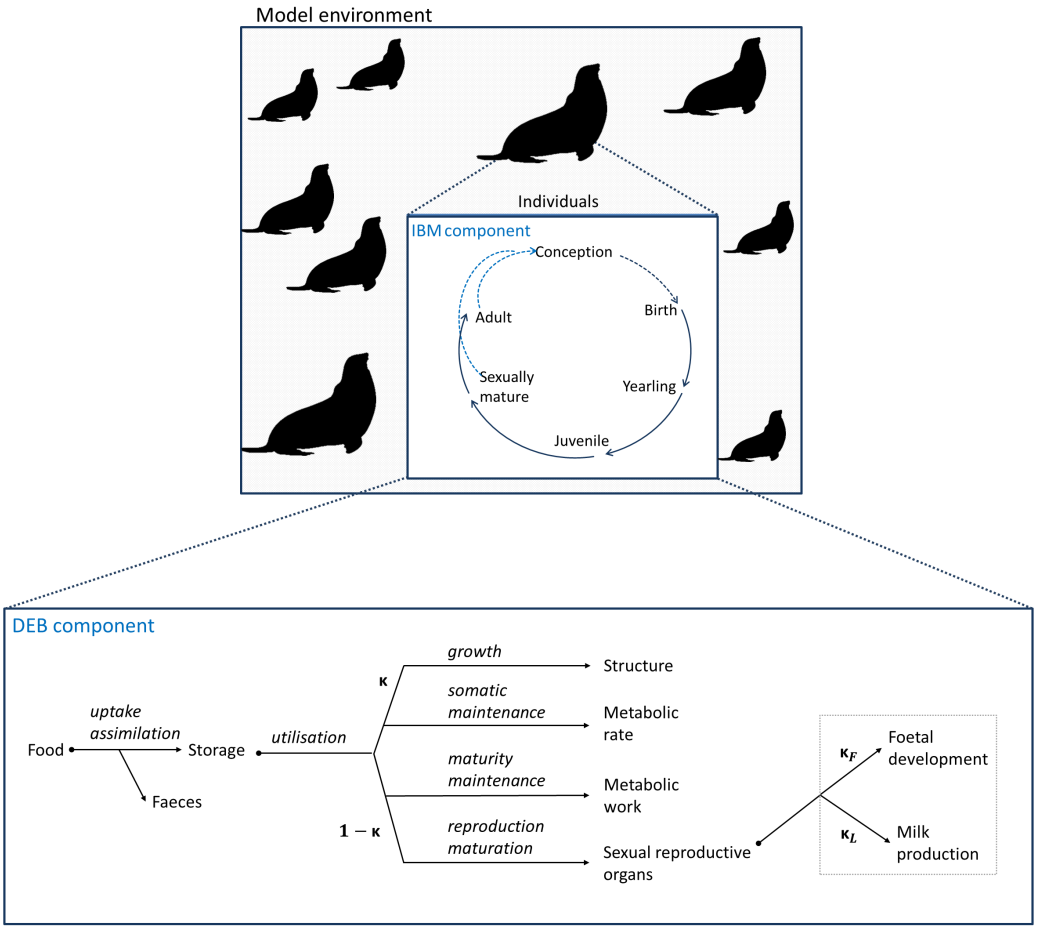

Figure 1.1. The DEB-IBM environment contains individuals of different age and stage classes. Each individual steps through their life-stages and behaviour through the stochasticity of the individual-based modelling (IBM) components; based on feeding and energy use determined by the dynamic energy budget (DEB) components. The DEB and IBM components (and all parameters) are further explained in Chapters 2 and 3.

1.2 The study species

Southern elephant seals (Figure 1.2) are large predatory marine mammals, with circumpolar prey fields and breeding grounds on sub-Antarctic islands. They are one of few species who are extreme capital breeders; they accumulate energy prior to breeding, before provisioning

young by using those storages during a three to four week fast (Drent and Daan, 1980; Costa and Shaffer, 2012). This means that during the weaning period, they do not re-enter the water to forage.

Figure 1.2. A southern elephant seal *Mirounga leonina* hauled out near Davis station, Antarctica. ©Merel Goedegebuure, 2016.

The global population of southern elephant seals is estimated to be stable at just under 750 000 individuals (Hindell et al., 2016). These estimates have increased in recent years following recovery from commercial exploitation, during which more than 1 million southern elephant seals were harvested (Laws, 1994). There are four genetically distinct sub-populations of southern elephant seals in the southern ocean, of which the largest population is at South Georgia Island, south Atlantic Ocean (∼413 671); with smaller sub-populations on Kerguelen and Heard Islands, south Indian Ocean (∼219 157); Macquarie Island, south Pacific Ocean (∼60 561), and; Peninsula Valdés, Argentina (∼56 000) (McMahon et al., 2005a; Hindell et al., 2016, and references therein). Population status (between the 2000s and 2010s; McMahon et al., 2005a; Hindell et al., 2016), is not uniform across the sub-populations. The population at Peninsula Valdés, Argentina, has increased while the sub-populations at South Georgia and the Kerguelen Islands have remained relatively stable (McMahon et al., 2005a,b; Hindell et al., 2016). The southern elephant seal population at Macquarie Island stands out as it has been in decline since the 1950s following recovery from commercial exploitation

(McMahon et al., 2005a; van den Hoff et al., 2014; Hindell et al., 2016, 2017), with an estimated annual decline in the population of ∼1.45% (Hindell et al., 2017).

Southern elephant seals from Macquarie Island forage in the South Pacific and South Indian regions of the Southern Ocean, with the majority of the trips heading to the Subantarctic and Polar fronts, or further south, past the Southern Antarctic Circumpolar current, to the ice edge of Antarctica (see O'Toole et al., 2015; Hindell et al., 2016, 2017, see Figure 1.3 for locations of frontal zones in respect to Macquarie Island), and return to the same locations for foraging over different years (Bradshaw et al., 2003). This site fidelity means that any changes in their prey field between years has the potential of affecting their energy intake and expenditure during foraging trips (Bailleul et al., 2007; Biuw et al., 2010). This is particularly important on foraging trips post breeding and post moulting where seals need to gain the weight they lost over the preceding weeks (O'Toole et al., 2015). There are a number of theories behind the observed population decline of the southern elephant seals at Macquarie Island, which have been a part of longitudinal studies (McMahon et al., 2005b; Hindell et al., 2017). Increased female mortality together with reduced recruitment may be a driver of the population's observed decline (van den Hoff et al., 2014). The increase in mortality and reduction in recruitment may be due to climate variability at the seal's foraging grounds (McMahon et al., 2003; van den Hoff et al., 2014). This climate variability (*e.g.* changes in the frequency and intensity of El Niño Southern Oscillation (ENSO) events, or a tendency to a more negative Southern Oscillation Index) may be impacting the food availability, which is a determinant in the species growth, breeding success, and (juvenile) survival (see McMahon et al., 2000, 2005a; McMahon and Burton, 2005; van den Hoff et al., 2014; Clausius et al., 2017b).

1.3 Thesis approach

This thesis presents the first individual-based model incorporated with a dynamic energy budget for a large marine mammal that can follow individuals throughout their life cycle from birth to death. The DEB-IBM has been developed for southern elephant seals and we have shown that it can be used to project a stable population over time with realistic emergent life history and breeding behaviour for individuals (Chapter 3). We have also shown the use for the model as a predicting tool for population behaviour with implemented intrinsic and extrinsic changes (Chapter 4). Although the model has been developed as a stand-alone model for southern elephant seals we discuss how it can be modified to suit other higher

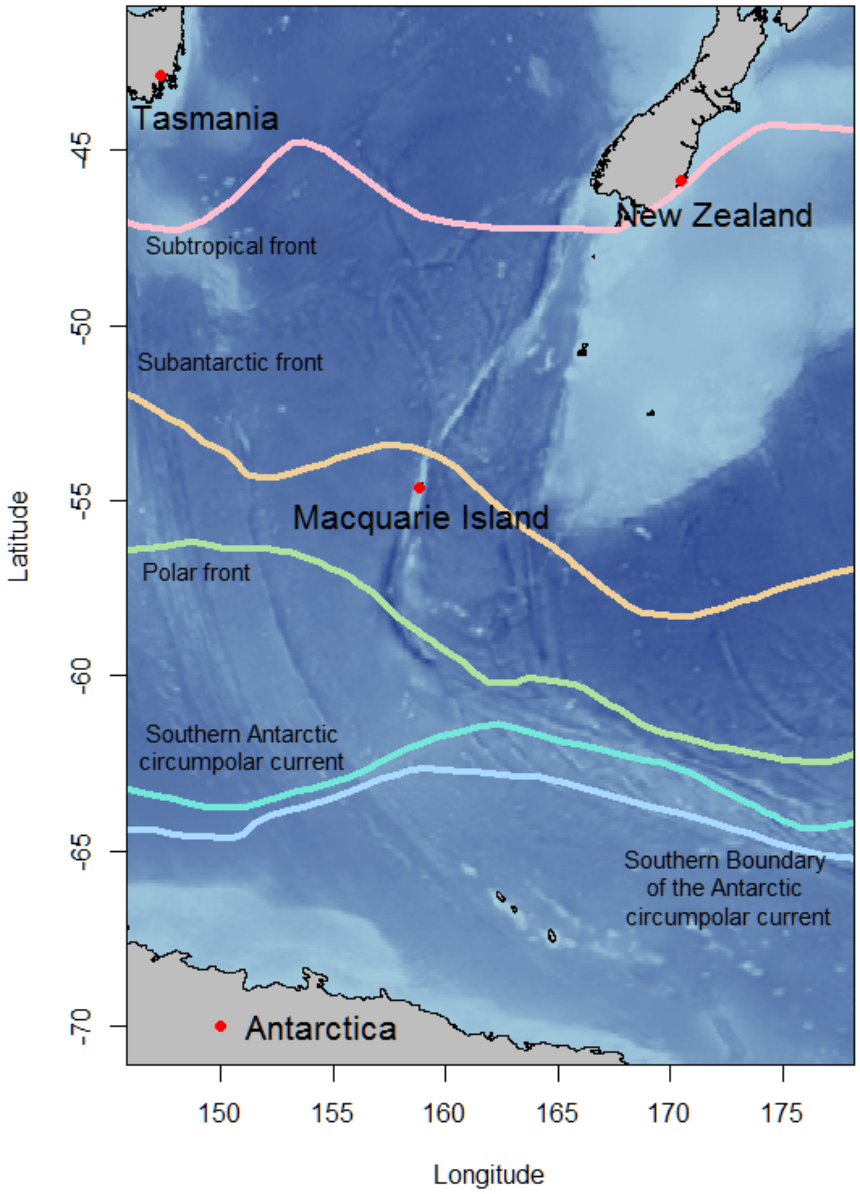

Figure 1.3. Map showing locations frontal zones (Subtropical front, Subantarctic front, Polar front, Southern Antarctic circumpolar current) in relation to Macquarie Island. The locations of Australia, New Zealand and Antarctica are for highlighted for reference.

trophic-level (marine) mammals and sea birds and that, ultimately, it can be incorporated into end-to-end ecosystem models to fill a gap in current research and end-to-end ecosystem

model development (Chapter 5).

Chapter 2 presents a review (Goedegebuure et al. (2017) *Ecol. Mod.* 359; doi.org/10.1016/j.ecolmodel.2017.04.004) on the current state and methods used for the representation of higher trophic level predators in end-to-end ecosystem models. This chapter highlights the limited methods used for representation of marine mammals and birds: many end-to-end ecosystem models only represent higher trophic-level predators using closure terms or simplified methods. The article summarises seven modelling frameworks used for the development of end-to-end ecosystem models, and for a selection of models within these frameworks, it highlights the model design; the included predator species; and the methods used for their representations.

To demonstrate the effects of the methods used for top predator representations (simple *versus* more detailed), we developed a nested qualitative network model to examine responses to perturbations in a simplified Southern Ocean foodweb. The model includes four levels of complexity, with two levels of top predator representations and a simple scenario (perturbation) representing environmental change. The results showed that the level of detail chosen for the modelling of higher trophic levels can have implications regarding model predictions.

The article concludes with a discussion on potential approaches to representing higher trophic level species with more detail in end-to-end ecosystem models. Although there were many different options used in the end-to-end models we analysed, none included the complex behavioural and breeding traits of predators, as well as their energetic requirements and uses. To include this in end-to-end ecosystem models we suggest incorporating dynamic energy budget theory with individual-based modelling (DEB-IBMs; Martin et al., 2012) to represent higher trophic level species in detail.

Chapter 3 describes in detail the DEB-IBM that was developed as the major component of this PhD project (Goedegebuure et al. (2018). PLOS ONE 13(3): e0194950 doi.org/10.1371/journal.pone.0194950). The aim of the development of the model was to show that DEB-IBMs can be developed for more complex higher trophic-level species while being able to i) simulate energy use and life histories, as well as breeding traits of southern elephant seals in an emergent manner ii) project a stable population over time, and iii) have realistic population dynamics and structure based on emergent life history features (such as age at first breeding, lifespan, fecundity and (yearling) survival).

As with any newly developed model, evaluation and sensitivity analyses were conducted to test the model limits, and better understand the results of simulations. For the sensitivity

analyses we modified parameters for resource availability, as well as transition thresholds for birth, weaning and puberty.

During the model evaluation, comparisons were made to real-life data collected from Macquarie Island (see *e.g.* McMahon et al., 2005b), which focus on life history and breeding behaviours such as pup and yearling survival; reproductive ages; juvenile, adult and transition ages; lifespan; breeding success and growth, as well as the population size and dynamics. These were all selected as not only can they be tracked in the model; the majority of these are known from studies on Macquarie Island.

Chapter 4 investigates a number of scenarios based on some of the more likely hypotheses surrounding the observed decline in southern elephant seal population on Macquarie Island, using the DEB-IBM introduced in Goedegebuure et al. (2018); presented in Chapter 3 of this thesis. The aim was to investigate if a DEB-IBM can be used to evaluate four hypotheses regarding the observed population decline on Macquarie Island through implementing scenarios of i) climate variability ii) reduction of yearling survival iii) reduction in the fecundity of mothers, and iv) density dependence in the model.

As previously mentioned, the southern elephant seal population at Macquarie Island has undergone significant changes, having virtually halved in size since 1949 (Hindell et al., 2017). The actual driver behind the population decline is unknown, and while emigration has been discounted there are a number of hypotheses about potential drivers. To test the abilities of our DEB-IBM we chose to test four of the hypotheses by implementing different scenarios to the model.

The first scenario implemented in the model looks at climate variability which directly affects the foraging grounds (and thus resource availability) of the southern elephant seals at Macquarie Island. We implement this in the model through representation of two climatic events; the El Niño Southern Oscillation, and the Southern Annular Mode. The second scenario implemented in the model looks at a reduction in yearling survival which is implemented through reductions in energy intake to a proportion of yearlings. The third scenario implemented in the model looks at a reduction in the fecundity of mothers which is implemented through an increase in the reproductive threshold of potential mothers. The fourth and final scenario implemented in the model looks at the effects of density dependence on the population, in relation to a reduced overall resource availability to all foraging individuals through a stepwise reduction of the carrying capacity of the model. We show that our model can be used to illustrate how each of these scenarios may result in distinct changes to the overall population and population structure and thus may be used to differentiate between

the different hypothesised drivers of the observed decline.

In **Chapter 5** we summarise and synthesise the preceding chapters to bring everything together. We use the results and limitations of the DEB-IBM to suggest some potential changes and recommendations for future development and implementations of the model.

Chapter 2

Beyond big fish: The case for more detailed representations of seabirds and marine mammals in marine ecosystem models

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Abstract

Seabirds and marine mammals are generally not well represented in marine ecosystem models, despite the important roles that these groups often play in determining ecosystem dynamics. This is an important gap in model development, particularly for end-to-end ecosystem models designed to look at ecosystem wide impacts, which are becoming increasingly important tools for fisheries and ecosystem based management and assessment. Examination of large-scale and widely-applied pelagic end-to-end ecosystem models indicates that representations of predators are currently best developed for fish groups. The methods for modelling seabirds and marine mammals on the other hand, are less well developed. This is potentially due to the challenges involved in data collection and in representing the complex life histories of many of these species. To examine the effect that different representations of higher trophic level

predators might have on ecosystem model predictions, we developed a set of simple nested qualitative network models and examined their responses to perturbations. Responses differed between models across a range of trophic levels under a simple scenario for environmental change, highlighting that how predators are modelled can have implications for ecosystem-level predictions. We conclude with a discussion around potential approaches for developing more detailed representations of predator groups, and suggest incorporating dynamic energy budget theory in individual-based models to represent higher trophic level predators with more complex life histories.

2.1 Introduction

Changing dynamics of top predators may signal lasting change in bottom-up forcing of marine ecosystems (*e.g.* Constable et al. (2014) for Antarctic ecosystems and Boaden and Kingsford (2015) for tropical reefs). This is because life time performance of individuals is an integration of short term variability in the system, and for top predators is reflected in longer term trends as a result of their comparatively longer lives (Hindell et al., 2003; Travers et al., 2007; Thompson et al., 2012). The slower response to change means that they may exert significant pressures on their environment and the ecosystem; directly through top down predation (Smetacek and Nicol, 2005; Sala, 2006; Heithaus et al., 2008; Estes et al., 2011; Boaden and Kingsford, 2015; Kiszka et al., 2015), and also through indirect effects (Trathan et al., 2007; Estes et al., 2011; Ruppert et al., 2013; Constable et al., 2014). Such effects may include behavioural avoidance by prey (Creel and Christianson, 2008; Heithaus et al., 2008; Kiszka et al., 2015), and facilitation of the recycling of nutrients, thereby enhancing carbon cycling (Atwood et al., 2015; Ratnarajah et al., 2016). There is also some evidence that predators can stabilise foodwebs, making these foodwebs more resilient to stress (Sala, 2006).

Despite the vital roles played by higher trophic level predators, these species are often not well represented in ecosystem models. This is particularly the case for seabirds and marine mammals whose complex life histories (Table 2.1), and as a consequence allocation of energy from prey, are difficult to model. Factors to consider when modelling these species are the dislocation of breeding sites from main foraging areas, combined with investment of energy in latent reproductive capacity, as well as parental care. These factors can contribute to complex predator-prey relationships which may not be easily represented through simple mortality rates for lower trophic levels. This is important as such changes in energetics and

behaviour of predators may play crucial roles in their demand for food, and their allocation and use of acquired energy. Complex representation of higher trophic level species are not needed in all models, particularly if addressing specific questions in well-defined scenarios (Starfield, 1997; Essington and Plagányi, 2014); indeed, simplified representations can lead to greater computational efficiency (see *e.g.* Fulton et al., 2003; Essington and Plagányi, 2014; Punt et al., 2016). However, further investigation is needed (see discussion in section 2.5) to check whether conclusions are likely to be robust to the representation of these predators; in other words, when might complexity matter?

Here, we examine the importance of including detailed and realistic representations of seabirds and marine mammals in marine ecosystem models, with a focus on end-to-end ecosystem models. We use a broad literature survey of commonly used approaches for representing higher trophic level predators in ecosystem models (Fulton, 2010; Murphy et al., 2012; Young et al., 2015, ; see section 2.2), highlighting examples of model frameworks which implement more detailed representations of top predators (Table A1; Fulton et al., 2004; Gray et al., 2006; Maury, 2010; Fiechter et al., 2016). We use a qualitative network model to demonstrate how a simplified representation of top predators may limit perspectives on ecosystem dynamics (Dambacher et al., 2002; Melbourne-Thomas et al., 2012, ; see section 2.3). Taking into consideration the key life history and reproductive traits of seabirds and marine mammals that are challenging to represent in models (Table 2.1), we suggest using individual-based models (IBMs) that incorporate dynamic energy budget (DEB) theory (Kooijman, 2010b; Martin et al., 2012, ; DEB-IBMs, see section 2.4), as a suitable modelling tool (see also Constable, 2005, on energetic modelling approaches) for representing these traits in ecosystem models. Here, we use the term 'ecosystem model' when referring to general representations of ecological systems and the term 'end- to-end ecosystem model' for representations of the combined physical, chemical, biological and human systems (Fulton et al., 2003; Fulton, 2010; Rose et al., 2010; Shin et al., 2010; Murphy and Hofmann, 2012).

2.2 Representations of predators in marine ecosystem models

The approaches used for representing predator species in end-to-end ecosystem models vary widely; from closure terms for their prey (*e.g.* quadratic mortality of prey representing consumption by predators without modelling predator populations; Fulton et al., 2003; Plagányi and Butterworth, 2004) through to complex behavioural models of predators along with their population dynamics to better represent consumption of prey by predators (*e.g.* Gray et al.,

Table 2.1. Key life history and reproductive traits of seabirds and marine mammals that are challenging to represent in models but can be captured using a DEB-IBM approach.

Top predator traits	**Implications for model (representations)**
Delayed and intermittent reproduction	▪ Depending on the species there might be a significant diapause in the breeding cycle. ▪ Not all species or even individuals will breed every year. Breeding is generally dependent on individual energy reserves allocated to reproduction, or could be dependent on environmental parameters in a selected year.
Distinct breeding behaviour of colony breeders	Colony breeders need to come on land for mating and raising their offspring ▪ Marine Mammals such as seals ▪ Return to the water after impregnation ▪ Females need to increase their food intake during pregnancy ▪ Females need to come on land for birth and fast during weaning. ▪ Seabirds such as penguins ▪ Come on land to lay eggs and fast while brooding ▪ Seabirds may swap roles between male and female over guard and crèche stages of breeding ▪ Increased intake of food needs to be accounted for, for both sexes during the guard and crèche stages ▪ Seabirds, as income breeders (see below) need to forage while providing for their chicks and thus have limited foraging ranges.
Distinct breeding behaviour of wholly pelagic predators	Wholly pelagic predators, such as whales, may not feed for a period of time while they are moving to, or in breeding grounds. This means that, in a model, energy budgets may need to be managed both inside and outside a given model domain.
Capital vs. income breeders (Houston et al., 2007)	Patterns of food intake during pregnancy (or egg production) and lactation/provisioning are most easily represented using a DEB-IBM approach. ▪ Capital breeders store energy for feeding offspring ▪ Income breeders forage and feed offspring concurrently
Prey selection behaviours	Many predators have the ability to switch prey under certain circumstances (e.g. Bedford et al., 2015). This allows them to maximise their energy intake, while minimising their energy expenditure (Watanabe et al., 2014; Bestley et al., 2015). While prey-switching can be represented functionally (Holling, 1965), DEB-IBMs provide more flexibility to represent prey selection behaviours.
Site fidelity (Arthur et al., 2015)	Some species, such as seals, exhibit strong site fidelity – which means that these individuals return to the same foraging grounds each year. This needs to be given consideration in models where environmental changes are represented spatially as this will have an effect on the available prey field to these individuals.

2006; Fiechter et al., 2016). Basing representations of top predators on mortality terms may be appropriate for a system where predator populations closely track prey populations in relative abundances. However, when systems are undergoing change due to external forces (such as changes to fisheries or climate) the underlying spatial and temporal patterns between components may change (Guisan and Zimmermann, 2000), and result in different or even varying mortality rates of the prey.

To identify the commonly used approaches for including higher trophic level predators such as seabirds and marine mammals in marine end-to-end ecosystem models we conducted a broad literature survey. Here we summarise the approaches for representing higher trophic level predators in those models that do explicitly represent these species Table A1.

Ecopath with Ecosim (Christensen and Walters, 2004) models are integrated ecosystem models, which have been developed (ongoing) over more than thirty years (Polovina, 1984). A multitude of regional models have been developed, with the majority focussing on the effects of fisheries on a food web using a mass balance approach (Ecopath) with dynamic modelling (Ecosim). A number of these models include colony breeders as well as other top predators (*e.g.* Guénette et al., 2014; Gurney et al., 2014; Koehn et al., 2016). These species are represented as aggregate populations or functional group aggregates based on size, habitat use, diet, and fisheries or conservation considerations.

SEAPODYM (Spatial Ecosystem and Population Dynamics Model) (Lehodey et al., 2003; Lehodey, 2004; Lehodey et al., 2008; Dragon et al., 2015) is a coupled physical-biological interaction model, applied to fish predators (tuna species). Tuna are represented using age-structured populations. The mortality terms applied include natural mortality (for juveniles only) and fishing mortality (to all age classes). The model has been developed for the Pacific Basin and in its latest framework can distinguish between environmental and fishing effects for spatialized management advice (Dragon et al., 2015).

OSMOSE (Object-oriented Simulator of Marine Ecosystem Exploitation) (Shin and Cury, 2001, 2004) uses IBMs to represent piscivorous and non-piscivorous predators for the Southern Benguela ecosystem, South Africa. Further development of OSMOSE includes coupling with ROMS (Regional Ocean Modelling System; a hydrodynamic model) and a NPZD (Nitrogen, Phytoplankton, Zooplankton, Detritus) sub-model (Travers-Trolet et al., 2014b,a). This model assumes size-based opportunistic predation, with birds and marine mammals represented as global predation mortality terms.

Fiechter et al. (2015) and Rose et al. (2015) developed a coupled NEMURO (North Pacific

Ecosystem Model for Understanding Regional Oceanography), NPZ and IBM end-to-end ecosystem model to understand trophic interactions and the effects of habitat utilisation in the California Current System. Their target species (anchovy and sardines) are modelled using detailed IBMs, and the predator (Albacore tuna *Thunnus alalunga*) is included using a simplified IBM without aging or reproduction processes. A separate sub-model is included for fishing mortality on sardines. Recent additions to the model have included a detailed representation for top predators (Fiechter et al., 2016), using an IBM for California sea lions *Zalaphus californianus*. The coupled ROMS and NEMURO NPZD model represents forage fish (anchovy and sardines) as super-individuals (Scheffer et al., 1995) in IBMs, and simulates the foraging ecology of male California sea lions through individual IBMs which include a simplified version of a mechanistic dynamic model (Lavigne et al., 1986) for bioenergetics representation by balancing consumption, metabolism and waste.

APECOSM (Apex Predators Ecosystem Model) (Maury et al., 2007a,b; Maury, 2010) has been developed to model environmental influences on marine ecosystem dynamics. The model includes dynamic energy budget theory (Kooijman, 2010b) to represent the energy flows through a pelagic ecosystem, applied to predators (here, four tuna species). Predation by the target species is represented using opportunistic size-based approaches. The mortality terms applied to tuna cover natural mortality (encompassing starvation and non-predatory) as well as mortality due to fishing.

Atlantis (Fulton et al., 2004) has the ability to represent mid-to high trophic levels as aggregated functional groups or to be resolved at species level as age-structured populations. This widely applied framework combines a number of sub-models that can be activated as required. An example of inclusion of top predators can be found in the Atlantis model for South East Australia (Fulton et al., 2007; Audzijonyte et al., 2014a,b; Fulton and Gorton, 2014) where vertebrate species are represented as age-structured populations. In this model, fish species are aggregated (except for those of particular interest to fisheries, which are resolved at species level), seals, dolphins and baleen whales are grouped, and sea lions and orcas *Orcinus orca* are represented as individual model components.

Arguably the most advanced end-to-end ecosystem model–in terms of representing species with complex life histories–is InVitro (Gray et al., 2006; Fulton et al., 2011; Gray et al., 2014; Fulton et al., 2015). This end-to-end ecosystem model combines sub-models (from biophysical to socio-economics and management, monitoring and assessment) for Ningaloo-Exmouth region in Western Australia. This modelling framework allows for the inclusion of meta-populations and IBMs, as well as additional natural and human induced mortality

terms. The Ningaloo-Exmouth InVitro model includes detailed IBMs for a number of turtle, manta ray, shark, whale, and dolphin species, and dugong *Dugong dugong*.

Overall, the majority of published marine ecosystem models focus on lower trophic levels or target fish (e.g. tuna), fisheries and fisheries management (see discussion above, and also Travers et al., 2007; Maury and Poggiale, 2013). These models often represent top predators through age- and stage-based approaches (Rose et al., 2010) or single demographically unstructured guilds (Heath, 2012; Morris et al., 2014). For end-to-end models we surveyed, the level of detail on how higher trophic level, non-target species were represented was variable, which is perhaps unsurprising given that these models have varying purposes and were generally not developed around questions specifically targeting higher trophic level predator species.

2.3 The effect of representing predators at varying levels: a case for more details

More complex representations of top predators will usually increase the cost associated with development and use of these models. Fulton et al. (2003) suggest that the predictive capacity of ecosystem models is highest at some intermediate level of complexity. Thus identifying an optimal level of detail or complexity in an ecosystem model is an important, yet challenging factor in the process of developing models. In this regard, an important question is 'What level of detail in the representation of top predators is needed for an end-to-end ecosystem model to be fit for purpose?'. In this section, we use qualitative network models for a relatively simple Southern Ocean pelagic foodweb to demonstrate how changes in representation of higher trophic level functional groups can affect model outcomes.

Qualitative network modelling provides a relatively simple demonstration of ecological feedbacks and foodweb responses to perturbation, without the fine details that are needed for more comprehensive, quantitative ecosystem models (Levins, 1966; Dambacher et al., 2002; Melbourne-Thomas et al., 2012). Links between components within a system are represented directionally as positive ($\rightarrow$) or negative ($\blacksquare$) interactions (Figure 2.1). Uncertain (or weak) linkages are represented as dashed (- - -) lines. Responses of the model to perturbations are evaluated through qualitatively specified community matrices, which capture the interactions between components within a system based on the signs of the linkages in the model ($\rightarrow$= 1, $\blacksquare$ = -1, and no link = 0) (Dambacher et al., 2002). The inverse of these matrices predict

the ultimate effect of a press perturbation on all community members by estimating the change in equilibrium following a perturbation (Dambacher et al., 2002).

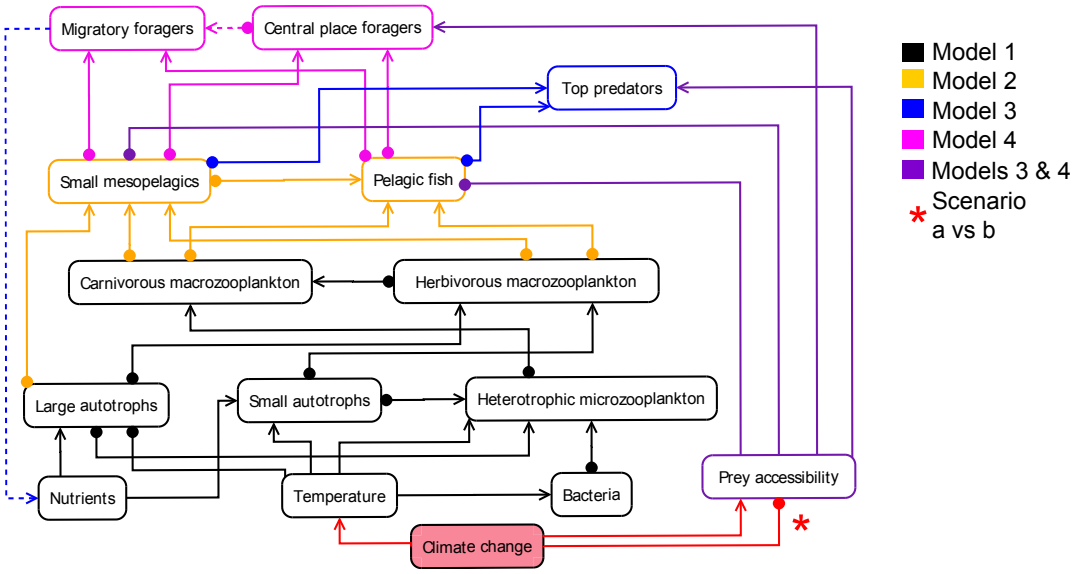

Figure 2.1. Nested qualitative network model representing a generalised Southern Ocean pelagic foodweb. Linkages between model variables represent positive ($\rightarrow$) and negative ($\blacksquare$) effects. Uncertain linkages are represented by dashed lines (the uncertain linkage from pelagic predators to nutrients follows the current research of the roles whales play in increasing the amount of bio-available iron (*e.g.* Ratnarajah et al., 2016)). Self-limitation (Dambacher et al., 2002) is applied to all variables. These nested models capture four levels of complexity: Model 1 (represented by the black components) represents a biogeochemical model; Model 2 (both black and yellow components) includes the biogeochemical model and a mid-trophic level; Model 3 (black, yellow and blue components) includes the addition of a generalised top predator (here assumed to be a combination of colony breeders (e.g. seals, penguins) and pelagic predators (e.g. whales, orcas)); Model 4 (black, yellow, blue and pink components) separates the top predators into two specific groups (colony breeders and pelagic predators). A positive perturbation in climate is applied to all four models through an increase in temperature; additionally, in Models 3 and 4 this perturbation also impacts the accessibility of prey to top predators. The single asterisk (*) indicates that scenarios are simulated for positive (a) and negative (b) effects of a positive perturbation in climate change on prey accessibility in Models 3 and 4.

Melbourne-Thomas et al. (2012) describe a simulation approach to qualitative network modelling in which interaction weights are randomly assigned from a uniform distribution (values between -1 and 1). Eigenvalues of each simulated (quantitatively specified) community matrix

determine its stability (see Melbourne-Thomas et al., 2012); unstable matrices are discarded while stable matrices are used for predictions of the modelled system to the applied perturbations. The sampling procedure is repeated until a pre-determined number of simulations have been achieved. Further details on model simulations and methodology can be found in (Melbourne-Thomas et al., 2012).

We developed a series of nested qualitative network models with four levels of increasing complexity (Figure 2.1): the first is a biogeochemical model (including nutrients, bacteria, two autotroph aggregates and three zooplankton aggregates); the second model includes mid trophic levels (small mesopelagics and pelagic fish); the third model includes a generalised top predator (colony breeders and pelagic predators are combined); the fourth model includes a more detailed representation of top predators (colony breeders and pelagic predators are separated into two groups). Self-limitation (Dambacher et al., 2002) is applied to each variable in the model, which captures un-modelled, limiting processes such as predation for variables without explicit predation from higher trophic levels (Model 1, 2). We applied a positive perturbation in 'climate change' (a broad term which includes environmental changes that affect foodwebs following an increase in overall temperature) to each model. The variable 'prey accessibility', introduced in Model 3, represents the 'ease' (or energetic cost) with which top predators can access and consume their prey (small mesopelagics and pelagic fish). This variable modifies the interactions between predator and prey through multiplications of the signs in the matrix (Dambacher and Ramos-Jiliberto, 2007). In our models, prey accessibility is directly influenced by either a positive or negative effect of a positive perturbation in climate change (scenario a vs b; Figure 2.1). Here, a negative effect of climate change on prey accessibility decreases the accessibility of prey to predators, while a positive effect of climate change on prey accessibility increases the accessibility of prey to predators. The prey accessibility as represented in Model 3 has a different effect on colony breeders compared with pelagic predators; pelagic predators have the ability to forage in a range of locations and are not as limited by changes in their prey-field. Therefore, in Model 4, the effects of prey accessibility are only applied to colony breeders as these are limited in their possible foraging distances during the breeding season because of the need to return to land to breed or feed offspring (*e.g.* Bedford et al., 2015). An example of a negative effect of climate change on prey accessibility is where climate change might cause a range shift (Bates et al., 2014) in target prey species, forcing predators to travel further from colonies to access prey. Conversely, a positive effect of climate change on prey accessibility might arise where a decrease in sea-ice extent means that prey are more accessible to predators at key times of year (Constable et al., 2014).

Analyses were conducted in *R* (version 3.3.2; R Core Team, 2016) following the method of Melbourne-Thomas et al. (2012) and results are visualised using the method described by Marzloff et al. (2016). Results from 1000 simulation runs of the qualitative network model under a positive perturbation to climate change (Figure 2.2) show that an increase in complexity of predator representations can influence ecosystem responses to applied perturbations. Model 1 presents a comparison in the form of a null case where no higher trophic level predators are included (biogeochemical model). Further model comparisons show varying ecosystem responses with the addition of predators at a range of complexities and trophic levels (Models 2, 3, 4). For example, with the inclusion of predation in Model 2 carnivorous macrozooplankton show a more positive response to a positive perturbation in climate change (Figure 2.2). The inclusion of higher trophic level predators in Models 3 and 4 introduces higher level feedbacks that also affect ecosystem responses to perturbation. Specifically, the response of pelagic fish changes from ambiguous (Model 2) to negative (Models 3a, 4a), when predators are introduced (or positive in Models 3b, 4b, following a negative prey accessibility to higher trophic level predators). Large and small autotrophs appear to show less pronounced (more ambiguous) responses to climate change in models that include top predators.

The responses of top predators themselves depend strongly on the complexity with which they were represented; there is a clear difference between the responses of a generalised top predator (Models 3a, 3b) and the response seen when the top predator group is partitioned between those with unrestricted pelagic foraging and those restricted to colonies during breeding (Models 4a, 4b) given a positive perturbation in climate change. Comparison of the representations of top predators at two levels of complexity (Models 3, 4) indicates that the combined, more general, representation of top predators (Model 3a) show an ambiguous response to the applied perturbation in climate change. Whereas colony breeders and pelagic predators, when separated (Model 4a), show distinctly different responses to the positive perturbation in climate change. The model simulation indicates that a positive perturbation in climate change has a positive effect on colony breeders, but a negative effect on pelagic predators.

Results of model simulations with positive perturbations in climate change in combination with a negative effect on prey accessibility (Model 3b, 4b) indicate an overall negative response by top predators (Model 3b), whereas for the more detailed representation of top predators, only the colony breeders reflect this response (Model 4b). Pelagic predators respond ambiguously to a positive perturbation in climate change combined with a negative effect on prey accessibility.

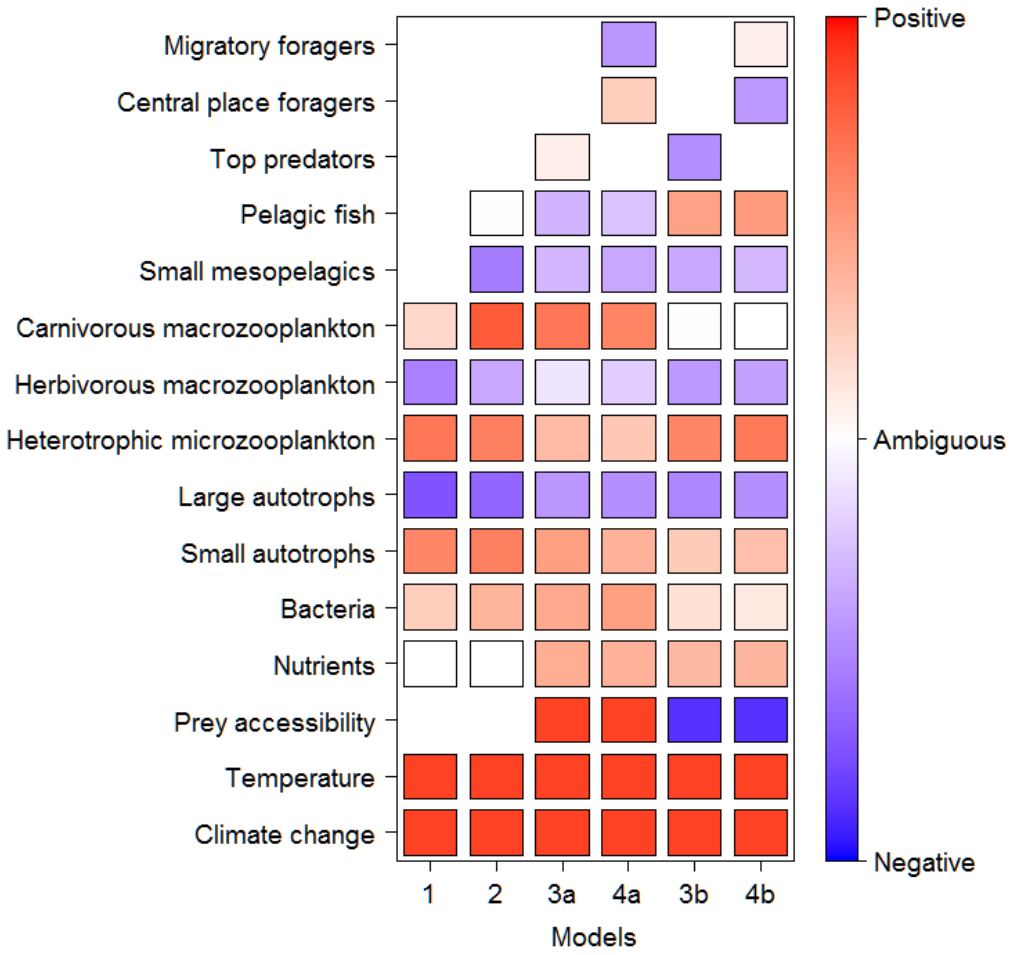

Figure 2.2. Results from 1000 simulation runs of the nested qualitative network models, as presented in Figure 2.1. The results show the probability of a positive (red) or negative (blue) response to a positive perturbation to climate change. Variable and Model names match those in Figure 2.1; note that the top predators for Model 3 are a generalised combination of colony breeders and pelagic predators (Model 4). The effect of climate change on prey accessibility is applied to Models 3 and 4; where 3a, 4a represent a positive effect, and 3b, 4b represent a negative effect. White boxes represent ambiguous results over all simulations (i.e. half positive and half negative results from simulation runs), and the grey represent zero change in response to a perturbation in climate change (i.e. no effect on nutrients in Models 1, 2).

While qualitative network modelling can capture feedbacks, a limitation of this approach is that it does not directly capture non-linear responses, such as prey-switching behaviours by predators. We note that our models are therefore conservative as these non-linear responses

may result in increased differences between different model formulations. Regardless, the examples of our simple qualitative network model show that representing top predators as a single group can lead to different ecosystem-level responses to climate change than when they are more explicitly modelled. Thus, the level of detail with which top predators are represented in ecosystem models can influence predictions of ecosystem responses to perturbations (see also Fulton et al., 2003).

2.4 Representing predators in detail through implementation of DEB-IBMs

Our analysis of commonly used approaches for representing predators in end-to-end ecosystem models highlights that higher trophic level predators with complex life histories are often not well represented in these models. The network modelling we have conducted demonstrates that ecosystem-level outcomes from models in response to perturbations are likely to be dependent on the complexity of the representation of top predators. Consequently it is important to assess whether top predators such as seabirds and marine mammals are represented with sufficient detail for model outcomes to be fit for purpose.

The predator-prey relationships that are important to capture in models relate to the strength of predation per capita (availability/accessibility of prey, behaviour and consumption rates of predators) and the abundance of predators. In order to satisfactorily represent top down effects, i.e. the mortality of prey, it will be important to capture when either of these may change over time.

Dynamics of populations are driven by life histories (key life stages) and breeding behaviours. These can be challenging to represent, particularly for land-based breeders. For example females may choose not to breed every year; energy intake and use changes when individuals fast during moulting, birthing, or weaning; individuals may exhibit site fidelity (Arthur et al., 2015) and be affected by localised prey depletion or other environmental changes. Individual-based models (IBMs, or agent-based models: ABMs) can be used to more closely represent complex life histories and behaviours. These models represent autonomous individuals, where each individual (or agent) has their own characteristics and goals to pursue (DeAngelis and Mooij, 2005; Grimm et al., 2005; Macal and North, 2010; DeAngelis and Grimm, 2014). Typically, IBMs are used to more closely represent a species interaction with the ecosystem through representing behaviour in response to habitat or system cues (Hindell et al., 2011;

Raymond et al., 2014; Young et al., 2015); the linkages of individual components within that system (Grimm, 1999); and to address complex, multi-level interactions within the system (Grimm et al., 2005; Railsback and Grimm, 2011), such as competition and prey-switching. These models are well suited for a range of different species, including high trophic level predators, and are becoming common tools for including behaviour and multiple life stages in ecosystem models (see Grimm, 1999; Thiele et al., 2011). In ecology, IBMs have been developed in a range of fields (see reviews by Grimm, 1999; DeAngelis and Grimm, 2014).

Although there has been an increase in the development of IBMs for fish species there are still very few models that have been developed for seabirds and marine mammals. Bailleul et al. (2013) used IBMs to study the migration phenology of beluga whales *Delphinapterus leucas* in the Arctic. Salihoglu et al. (2001) used an IBM to show the importance of food quality and quantity in determining the ability of Adélie penguin *Pygoscelis adeliae* chicks to reach optimum fledging weights, in spite of variability in Antarctic krill *Euphausia superba* abundance during the breeding season. These two models indicate the different levels of detail which can be used in IBMs, and show how IBMs can be used as standalone models to represent colony breeding and pelagic predators for studies specifically focussing on the selected species. With regards to ecosystem based management (*e.g.* Horne et al., 2010), these models would ideally be included in broad scale frameworks, such as end-to-end ecosystem models, that encompass multiple species. A recent example of this development is applied by Fiechter et al. (2016) for the representation of male California sea lions in the California Current.

The suitability of IBMs for more realistically representing higher trophic levels make them a useful tool for further development of predator representations in end-to-end ecosystem models. A recent review by Sibly et al. (2013) on including energy budgets in IBMs identified the Dynamic Energy Budget (DEB) theory (Kooijman, 2010b; Sousa et al., 2010; Jusup et al., 2017) as an effective approach to model the use and flow of energy by individuals. The theory aims to understand the dynamics of biological systems, from cells to ecosystems, via a balanced approach for mass and energy (Kooijman, 2010b; Martin et al., 2012). This is achieved by considering the assimilation and energy use of an individual organism for growth, maintenance and reproduction (van der Meer, 2006; Kooijman, 2010b; Nisbet et al., 2012; Martin et al., 2013) throughout its life-cycle (Figure 2.3). Maury (2010) successfully implemented DEB theory in the development of APECOSM for the representation of large predatory fish (tuna species) through a size based approach in an open ocean ecosystem model.

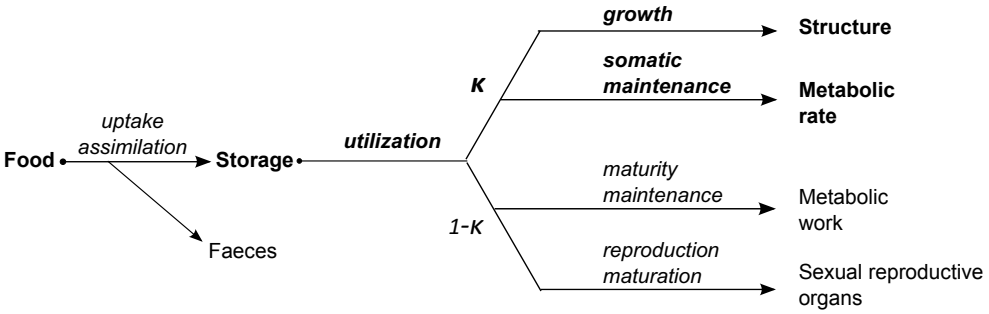

Figure 2.3. A dynamic energy budget model representation (adapted from Kooijman, 2010b) for a general organism. Food is ingested; energy is extracted and added to the reserves (storage), and utilised for; growth; somatic maintenance; maturity maintenance, and; reproduction maturation. Absolute priority is given to energy allocation for growth and somatic maintenance (κ). Any 'left over' energy (1 - κ) is utilised for maturation (embryos and juveniles) or reproduction and maturity maintenance (adults) (kappa rule Kooijman, 2010b).

Dynamic energy budgets can be incorporated into individual-based models to form a generic modelling framework, called DEB-IBM (Martin et al., 2012). By itself, DEB theory uses a deterministic approach, however, in combination with IBMs, DEB-IBM allows for the inclusion of stochasticity to provide a framework for investigating effects at a population level (Martin et al., 2012). The DEB-IBM approach has been used previously for studies on low trophic levels (e.g. rotifer (zooplankton) cultures (Alver et al., 2006) and water-flea species (Kooijman et al., 1989; Martin et al., 2013)), however this approach is yet to be applied to higher trophic levels. A template designed by Martin et al. (2012) bases representations of individuals on well-tested physiological principles and uses DEB theory in a population context. Considering the ability to analyse population characteristics and predator-prey interactions when combining DEB theory and IBMs (Martin et al., 2012) and the ability to include the complex life histories and breeding behaviour of seabirds and marine mammals, we propose that representations of top predators in ecosystem models could be greatly improved through implementation of DEB-IBMs.

2.5 Synthesis and future work

Although top predators play important roles in ecosystem function, for example through top down control or by their abilities to increase ecosystem stability, detailed representations of these species in ecosystem models are uncommon. Through our survey of commonly used approaches for representing top predators in end-to-end ecosystem models we demonstrated that there has been limited development of end-to-end ecosystem models with regards to specific (and realistic) inclusions of top predators such as seabirds or marine mammals (however, see *e.g.* InVitro).These species are often only represented through simpler methods or closure terms.

The issue of unnecessary complexity in ecosystem models has been discussed by several authors in multiple contexts. We argue that the simplification of the representation of high trophic level predators can limit the ability to capture the changing dynamics imposed on the system by changing external pressures such as climate change or fisheries. This is specifically the case where predators (or functional groups) are included as aggregates in models where individuals would behave in a variety of ways, and can have separate impacts on lower trophic levels or overall ecosystem structure. It is important to understand the relative behaviours of species in an ecosystem, especially under different scenarios. If the relative behaviour is altered substantially under different circumstances (such due to changes in climate) then the level of detail with which species are represented in models matters. As end-to-end ecosystem models become increasingly important ecosystem and fisheries management and assessment tools, it is important to recognise that model responses and predictions of ecosystems to particular perturbation scenarios could be significantly altered depending on the complexity and realism in the representation of different species.

The predictive power of models regarding ecosystem responses to environmental change and human activities will likely be diminished when model components are not represented with adequate detail. As such it is important to address questions regarding the appropriate detail needed in any given model. Specifically for models where representations of predators are in line with objectives, it is essential to investigate how a more realistic approximation of top predator populations can be implemented while maintaining computational efficiency. As a community we must learn how we can develop ecosystem models that represent the complex dynamics of higher trophic level predators in marine ecosystems and include the important flow of matter and energy throughout food webs without our models becoming overly complex and (computationally) expensive. For cases where representations of higher

trophic level predators are important, we believe that adopting the DEB-IBM framework is a useful approach. The framework allows for inclusion of autonomous individuals, and a detailed flow of energy throughout an individual's life cycle and is therefore well suited to model seabirds and marine mammals with complex life history and reproductive traits.

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Chapter 3

Modelling southern elephant seals *Mirounga leonina* using an individual-based model coupled with a dynamic energy budget

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Abstract

Higher trophic-level species are an integral component of any marine ecosystem. Despite their importance, methods for representing these species in end-to-end ecosystem models often have limited representation of life histories, energetics and behaviour. We built an individual-based model coupled with a dynamic energy budget for female southern elephant seals *Mirounga leonina* to demonstrate a method for detailed representation of marine mammals. We aimed to develop a model which could i) simulate energy use and life histories, as well as breeding traits of southern elephant seals in an emergent manner, ii) project a stable population over time, and iii) have realistic population dynamics and structure based on emergent life history features (such as age at first breeding, lifespan, fecundity and (yearling)

survival). We evaluated the model's ability to represent a stable population over long time periods (>10 generations), including the sensitivity of the emergent properties to variations in key parameters. Analyses indicated that the model is sensitive to changes in resource availability and energy requirements for the transition from pup to juvenile, and juvenile to adult stage. This was particularly the case for breeding success and yearling survival. This model is suitable for use as a standalone tool for investigating the impacts of changes to behaviour and population responses of southern elephant seals.

3.1 Introduction

Models are important tools for understanding and predicting changes in ecosystem state, and informing management (*e.g.* Murphy and Hofmann, 2012; Murphy et al., 2012; Xavier et al., 2016). However, the optimal level of detail with which to model specific ecosystem components depends on the aim of the model; detailed representations of ecosystem components can increase the cost associated with development and use of models, and intermediate levels of complexity can improve the predictive capacity of models (Fulton et al., 2003). Deciding on the necessary level of complexity required in a model is important; recent work has shown that the level of detail used for representations of higher trophic-level species such as seabirds and marine mammals can alter ecosystem-level responses to change, and can influence model predictions for single- (Punt et al., 2011; Gårdmark et al., 2013) and multi-species models (Goedegebuure et al., 2017). In this regard, to achieve effective ecosystem based management, models should ideally be developed in such a way that the representation of individuals can be used for population and ecosystems ecology (Grimm et al., 2017). Moreover, when developing a model to examine likely outcomes of future scenarios, or for conservation and management purposes, adding detail on the target species is an important consideration, particularly as behaviour (both that of the individual, as well as that of the population) and energy intake and expenditure are factors that are known to be influenced by environmental changes (see Southwell et al., 2015). Consequently, an essential component to ecosystem based management is the ability to quantify prey consumption by predators as this information can be used in the development of broader scale ecosystem models and management approaches see (see Murphy et al., 2012; New et al., 2014; Southwell et al., 2015).

There have been a range of single-species models with bioenergetics components developed for marine predators. Langton et al. (2014) developed an individual-based model (IBM: Grimm et al., 2005; Railsback and Grimm, 2011) for the common guillemot *Uria aalge*.

This model includes fine scale energetic representations for adults and their chick during the breeding season to address theoretical ecological questions and inform marine spatial management. Pavlova et al. (2014) designed an IBM to estimate food consumption by polar bears *Ursus maritimus* using known blubber content of East Greenland seals (the main prey species), and provide insight into polar bear energetics. Southwell et al. (2015) developed a bioenergetics model for Adélie penguins *Pygoscelis adeliae* to predict prey consumption during their breeding season. Bejarano et al. (2017) developed a conceptual bioenergetics model to estimate energy requirements of the bottlenose dolphin *Tursiops truncatus*, which includes estimation of prey biomass consumption using three different methods.

To improve the detailed representation of energetic use by species, and to explore population wide responses to perturbation, the use of DEB-IBMs (*sensu* Martin et al., 2012) has been suggested for representation of higher trophic-level predators with complex life histories (Pethybridge et al., 2013; Goedegebuure et al., 2017). These models incorporate dynamic energy budget (DEB) theory (Kooijman, 2010b; Sousa et al., 2010) within IBMs. Dynamic energy budget theory Kooijman (2010b) uses a deterministic approach to model the use and flow of energy by individuals and incorporates an individual's assimilation and energy use for growth, maintenance, and reproduction (van der Meer, 2006; Kooijman, 2010b; Nisbet et al., 2012) throughout its life-cycle (see also review by Jusup et al., 2017)). Individual-based modelling enables the study of individual interactions, system behaviours and complex multi-level interactions within the system (Grimm, 1999; Grimm et al., 2005; Railsback and Grimm, 2011; DeAngelis and Grimm, 2014).

The DEB-IBM framework combines the deterministic aspects of DEB theory (Fig 3.1) and the stochasticity of IBMs to study effects at a population level (Martin et al., 2012). It is based on well-tested physiological principles to represent individuals throughout their life cycle, and has been applied to a number of species including water-fleas *Daphina magna* (Martin et al., 2012, 2013; Goussen et al., 2016); oysters *Crassostrea gigas* (Bacher and Gangnery, 2006); zebrafish *Danio rerio* (Beaudouin et al., 2015); Antarctic krill *Euphausia superba* (Groeneveld et al., 2015), and anchovies *Engraulis encrasicolus* (Pethybridge et al., 2013).

As yet, no DEB-IBM has been specifically developed for mammals, however, the framework is well suited to model these species considering its potential to include complex life histories and breeding behaviour, as well as its ability to analyse population characteristics and predator-prey interactions Pethybridge et al. (2013). Thus, the goal of this paper is to demonstrate the use of DEB-IBMs for the detailed representation of a higher trophic-level predator. We

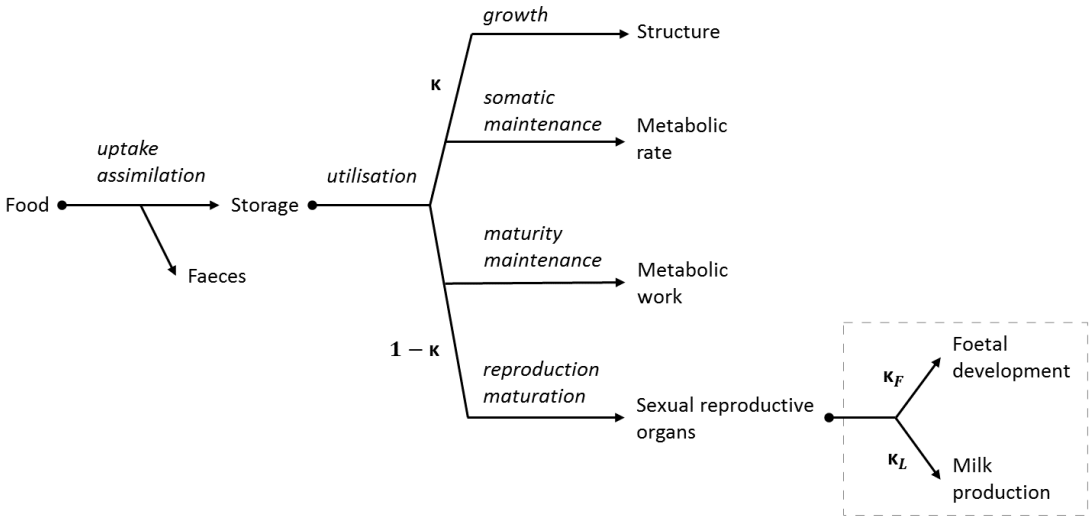

Figure 3.1. A dynamic energy budget model representation (modified from Goedegebuure et al. (2017), following Kooijman (2010b) and Roberts (2014)) for a general organism, with the additional resource allocation for foetal development, and lactation by mothers (dotted box). As food is ingested, energy is extracted and added to the reserves (storage). It is then utilised for growth, somatic maintenance, maturity maintenance, and reproduction maturation. The kappa-rule (Kooijman, 2010b) gives absolute priority to energy allocation for growth and somatic maintenance. While the remaining energy $(1 - \kappa)$ is utilised for maturation (embryos and juveniles), reproduction, and maturity maintenance (adults). Reproductive energy is allocated to foetal development κ_F, or milk production κ_L, depending on the pregnancy or lactation status of the individual.

present a DEB-IBM developed for female southern elephant seals *Mirounga leonina*; an abundant top predator of the Southern Ocean.

We included only female southern elephant seals in the model, as these make up the largest part of the population (Hindell, 1991, and Table A2), and are a crucial component in the survival of the species considering they singularly nurse their pups (as opposed to sharing this responsibility with a partner, as is the case for penguins, (*e.g.* Bedford et al., 2015)). The male population does not strongly influence the overall population trajectory (males make up only 36% of the adult population (Table A2), and only around 8% of males actually sire pups in a given year (which is based on the number of males over the age of 9, and the number of pups born in that year)). As such the population trajectory of southern elephant seals is only weakly dependent on the population size of males.

There are valid arguments as to why males should be included in population models for populations where male and female dynamics may differ (see Rankin and Kokko, 2007;

Gerber and White, 2014)—specifically for matrix population models and for understanding extinction risks—as opposed to assuming that populations can be represented based on females only (Caswell, 2001). However many of the arguments for including both sexes in population models assume that both sexes forage in similar environments, which is not the case for the majority of southern elephant seals (see Carrick et al., 1962; Campagna et al., 1999, for foraging and annual haul-out patterns). Additionally the assumption for having two-sex models for polygynous species, such as southern elephant seals has been shown to be important only when both male and female survival rates are low, as changes in male survival rates (when that of females stays high) has limited impact on population growth (Gerber and White, 2014); the survival rates of male southern elephant seals is significantly lower than that of females (Hindell, 1991).

As this DEB-IBM focusses on the population change over time, not just on the energy flow, we choose not to explicitly model male seals. For simplicity in the model it is assumed that all pups are born female, and remain female. Although at birth the ratio of males to females is equal, overall the population is comprised of approximately 36% males and 64% females (see Table A2, up to the age of 15 as this is the maximum observed age of male southern elephant seals). The energy that mothers expend on producing male pups at a ratio of 1:1 is accounted for in the model by increasing the breeding threshold (see section Thresholds for puberty, breeding and death in section 3.2), to ensure that we have (roughly) half the observed number of births.

Global numbers of southern elephant seals have increased in recent years following recovery from commercial exploitation, however this trend is not prominent in all sub-populations (McMahon et al., 2005a). The population at Macquarie Island has been in decline since the 1960s (McMahon et al., 2005a) at a rate of -1.45% per annum (Hindell et al., 2017). We have used the data collected from longitudinal studies on southern elephant seals on Macquarie Island for the model development. The specific aims of the study were to develop a DEB-IBM that could i) accurately simulate energy use, life histories and breeding traits of female southern elephant seals in an emergent manner, while ii) projecting a stable population over time, and iii) be used to evaluate the sensitivity of the emergent demographic properties to variations in key parameters.

3.2 Materials and Methods

Study species

Southern elephant seals forage throughout the Southern Ocean (McMahon et al., 2005a; Hindell et al., 2016) and are extreme capital breeders (they accumulate energy prior to breeding, and provision young by using only those stores (Drent and Daan, 1980; Costa and Shaffer, 2012)). They have pronounced sexual dimorphism (females up to 800 kg and 2.8 m in length; males up to 3000 kg and 3.5 m Laws, 1953; McLaren, 1993)). For females, breeding starts at the age of three (Laws, 1956), with optimal breeding after the age of four (Desprez et al., 2014), while somatic growth continues to the age of six (Laws, 1956; Desprez et al., 2014). Males reach sexual maturity at the age of five; however competition with more dominant bulls prevents these sub-adults from successfully mating. Somatic growth for males continues until seven years old, at which stage they may succeed in overpowering previously dominant bulls, creating a harem, and reproducing (Laws, 1956; McLaren, 1993). The maximum recorded age of female southern elephant seals is 23 years (Hindell and Little, 1988).

Female southern elephant seals breed between September and November and are impregnated while suckling their pup (Carrick et al., 1962). The pregnancy lasts for approximately 217 days, with implantation of the blastocyst delayed until February the following year, after the annual moult Laws (1984). While on land, and suckling her pup, the mother fasts for around 30 days (Laws, 1984). After weaning, the mothers return to the sea to replenish the energy they have lost (O'Toole et al., 2015). They return for a moulting period, 60-70 days later, in January (Carrick et al., 1962; Hindell and Burton, 1988b; McConnell et al., 2002). Fig 3.2 provides a detailed schematic of the relative energy use of a breeding female. Males arrive on land prior to the female's breeding period, and can stay there up to three months between early August and late October, depending on their success in gaining a harem. They then return for a moulting period between February and late April depending on age (older bulls first). Adult males are not seen on the island in winter (Carrick et al., 1962).

The pups weigh around 45 kg at birth, and 117 kg when they wean 23 days later (*e.g.* McMahon et al., 2000, 2017; Clausius et al., 2017b)). This rapid weight gain is possible due to the extreme 'fattiness' of southern elephant seal milk (16.1$\pm$6.98% fat on day one, up to 39.5$\pm$15.2% fat at weaning Hindell et al., 1994a). After weaning the pups stay on land for 4-5 weeks (Carrick et al., 1962) before going to sea to forage (Carrick et al., 1962). In winter,

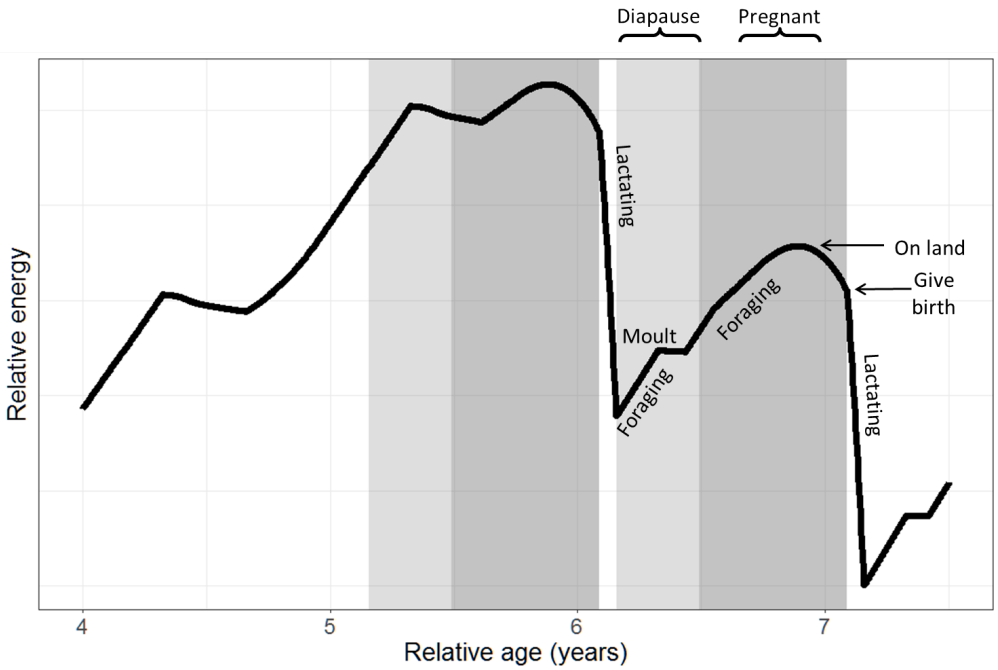

Figure 3.2. Model results for relative energy storage and use by an individual mother over two consecutive pregnancies. Relative age is included to show the timeframe before, during, and after pregnancies. Energy stores are depleted during fasting periods while the individual is on land (moulting and lactating), and are replenished during foraging trips (pre- and post-moulting periods). The reproductive energy storage U_R fluctuates with behaviour, and pregnancy requirements (as labelled). Grey background panels indicate stages of pregnancy: light grey indicates the period from conception to implantation (120 day diapause Laws, 1984); and dark grey indicates post-implantation (*i.e.* foetal development) period.

the juveniles return to land for a mid-year haul-out (Hindell and Burton, 1988b; McMahon et al., 1999).

Model details

Dynamic energy budget theory characterises individuals through descriptions of their *structure, reserves, maturity*, and *reproduction buffer*. *Structure* determines size, feeding rates and maintenance costs. *Reserves* account for energy storage, which is utilised following the kappa-rule Kooijman (2010b). The kappa-rule (Fig 3.1) states that absolute priority is given to the energy allocation for growth and somatic maintenance (κ). The remaining energy $(1-\kappa)$ is allocated to maturity, maturity maintenance, and reproduction. *Maturity* is a con-

tinuous state variable that regulates transition between stages at fixed levels. Here we use foetal, pup, juvenile, and adult stages to represent the seals, with transition parameters at birth, weaning and puberty, where puberty indicates the transition threshold between juvenile and adult stage and is solely reliant on the individual's energy storage, regardless of age or breeding status. *Reproduction buffer* is the energy stored for reproduction which is allocated to foetal and pup growth by pregnant or lactating individuals. The specific DEB rules regarding homeostasis and thermodynamics (Kooijman, 2010b) are covered in this DEB-IBM through utilisation of DEBtool for the collection of DEB state variables.

The DEB-IBM follows energy levels and behaviour of individual female southern elephant seals through their full life cycle, from conception to death. The start of the model requires a run-in period of approximately 50 years to allow for emergent properties of individuals to settle and for the model to reach a stable population. This run-in period allows for the 'first generation' seals to live, breed and die; the next generations start from conception, rather than estimated initialisation values, and become emergent model components. For simplicity, in the model set-up (see section Initialisation in section 3.2, below), 250 individuals are created, none of which start out pregnant or with offspring. The number of females with pregnancies or offspring thus becomes an emergent feature dependent on the levels of the mother's reproductive buffer.

The model runs on daily time-steps over a year, for a user-defined duration. We have used a 360 day annual cycle (*i.e.* each month consist of 30 days) as, considering the model does not include in-depth weather or other natural events, this approximation simplifies the model significantly. This modification also eliminates the need for implementation of leap years, which would add considerable complexity to the time frame of the individual based model. To account for a shorter year, we have modified the life cycle of southern elephant seals accordingly (including breeding, weaning and moulting times). Each seal still only breeds once per year and fasting, moulting and foraging occur at appropriate annual cycles. After set-up of the model, the 'daily' model process is applied as follows (Fig 3.3, and see section Sub-models in section 3.2, below for more details): i) as the date in the model is updated, each individual ages one day; the previous day's changes are reset to zero and the competition for food is recalculated based on the potential new population numbers, ii) each independent individual (those not reliant on their mother; thus excluding foetuses and pups) checks their activity and breeding status, calculates their changes in reserves, maturity or reproductive buffer, and length, and calculates their physical aging (due to the accumulation of damage inducing compounds (see Kooijman, 2010b)), iii) the calculated changes are implemented and energy levels are checked for survival, iv) juveniles transition to the next stage if energy

levels permit, v) pregnant mothers update their foetus' variables, vi) nursing pups calculate their changes in reserves, maturity and length, and update their variables and the reproductive buffers of lactating mothers are updated again (if pups have reached their energy threshold, they transition to juvenile stage), vii) all individuals apply age related mortalities for old age, or non-energetic mortality for yearlings (see section Sub-models, below), and viii) the model output is updated, and dead individuals are removed before the next time step begins.

Model description

The model description follows the ODD (Overview, Design concepts and Details) protocol for describing individual-based models (Grimm et al., 2006, 2010). The DEB-IBM was developed in the open-source agent-based modelling framework NetLogo (version 6.0.1 March 2017; Wilensky, 1999) for female southern elephant seals. We modified the scaled (see section Model modifications, below) framework built by Martin et al. (2012) for water fleas (NetLogo version 4.1.1, 2010) to fit southern elephant seals.

We follow the DEB notations for parameters, as per (Kooijman, 2010b,c; Martin et al., 2012); a full list of parameters used for this model can be found in Tables 3.1 and 3.2; published parameters for southern elephant seals from Macquarie Island were used for parameter settings of both the DEB and IBM components of the model.

Purpose

The purpose of this model is to provide a basic framework to represent higher trophic-level predators with complex life histories in a detailed fashion. The model includes detailed representations of energy requirements and use, as well as (breeding) behaviour.

Entities, state variables, and scales

For the development of the model, the DEB parameters were collected using the 'DEBtool' toolbox for Matlab (version R2014a 8.3.0.532; http://www.debtheory.org/; latest version downloaded on 19-07-2016, see also Appendix A2) to determine the state variables (defined by Kooijman (2010b) as a "variable which determines, together with other state variables, the behaviour of a system. The crux of the concept is that the collection of state variables,

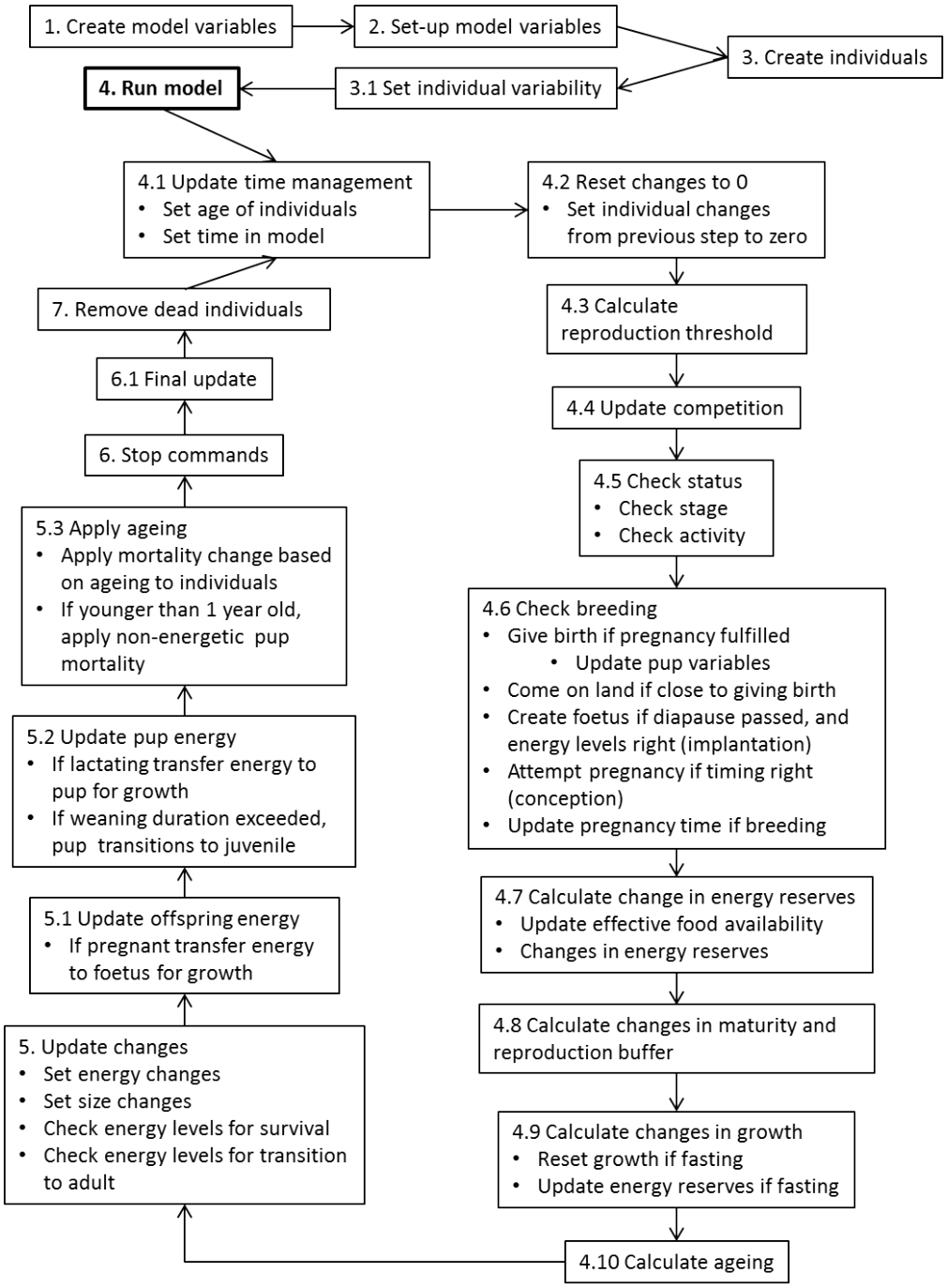

Figure 3.3. The set-up process of the model (steps 1-3), followed by the daily process (*i.e.* at each time-step) of the DEB-IBM for southern elephant seals (steps 4-7). Headings of steps 4-7 follow the headings of the sub-models as described in the ODD (Overview, Design concepts and Details) in section Sub-models in section 3.2.

Table 3.1. DEB parameters and state variables used in the baseline model initialisation. All parameters follow DEB notations. 'Entities' refer to the entities in the model that are impacted by the parameters; "G" for global, "I" for individuals. 'Change frequency' indicates how often the parameter changes; "-" indicates no change. 'Notes' hold references for values relating to the population dynamics of southern elephant seals, relevant equations for parameters, and further details on parameters: where a = DEBtool value; b = user defined during the model development stage; c = emergent model value.

DEB not.	Value	Units	Descriptor	Entities	Change freq.	Notes
cv	0.05	-	Initial individual variability	I	-	b
iv	-	-	Effective individual variability	I	At setup	eq 3.1
g	0.7138	-	Energy investment ratio	I	At setup	a
$\dot{\nu}$	0.065	cm d^{-1}	Energy conductance	I	-	a
$\dot{k}_M$	0.0014	d^{-1}	Somatic maintenance coefficient	I	-	a
$\dot{k}_J$	0.002	d^{-1}	Maturity maintenance coefficient	I	-	a
κ	0.74		Fraction of mobilised energy to			a
κ_F	0.725		soma (κ), foetal development (κ_F),	I	-	b
κ_L	0.02		and lactation (κ_L)			b
f_a	0.935	-	Absolute food availability	G	-	b
P	-	Individuals	Population	G	Daily	c
K	1000	Individuals	Carrying capacity	G	-	b
$\dot{p}_{Am}$	968.2785	J d^{-1} m^{-2}	Surface-area-specific maximum assimilation rate	G	-	a
δ_M	0.235		Shape coefficient	I	-	b
f_eff	-	-	Effective food availability	I	Daily	eq 3.2
ΔP	-	-	Competition	I	Daily	eq 3.3
L	-		Volumetric structural length	I	Daily	eqs 3.4, 3.18
L_b	110		Volumetric structural length at			see McMahon et al. (2000),
L_x	125	cm	birth (b), weaning (x),	I	-	McMahon et al. (2017),
L_p	180		puberty (p), and			Clausius et al. (2017b)
L_m	280		maturity (m)			
l	-		Scaled structural length	I	Daily	eq 3.6
E_H^b	2.81×10^7		Maturity threshold at birth (b),			a
E_H^x	6.50×10^7	J	weaning (x), and	I	-	b
E_H^p	1.45×10^8		puberty (p)			a
e	-	-	Scaled reserves per unit of structure	I	Daily	eq 3.8
U_H^b	2.90×10^4		Scaled maturity thresholds at			
U_H^x	6.71×10^4	-	birth (b), weaning (x),	I	-	eq 3.9
U_H^p	1.50×10^5		and puberty (p)			
U_E	-	-	Scaled reserve	I	Daily	c; eq 3.5
U_H	-	-	Scaled maturity	I	Daily	c; eq 3.9
U_cum	-	-	Cumulative energy req. for breeding	I	Annually	eq 3.10
U_R	-	-	Scaled reproductive buffer	I	Daily	c; eq 3.20
S_C	-	-	Mobilisation flux	I	Daily	eqs 3.11, 3.12
S_A	-	-	Assimilation flux	I	Daily	eqs 3.13, 3.14
$\ddot{h}_a$	6.0×10^{-10}	d^{-2}	Weibull ageing acceleration	I	-	a
s_G	0.1	-	Gompertz stress coefficient	I	-	a
$\ddot{q}$	-	d^{-2}	Ageing acceleration	I	Daily	eq 3.21
$\dot{h}$	-	d^{-1}	Hazard rate	I	Daily	eq 3.22

Table 3.2. IBM parameters as used in model initialisation. 'Notes' hold relevant equations for, and further details on, parameters: where a = user defined value; b = means taken and individual variability applied; eq 3.1; and c = value adjusted to fit 360 day model (see text).

IBM parameters	Value	Units	References	Notes
Individuals created at start of model	250	Individuals		a
Moult duration				
Pups	50	d		
Juveniles	26	d	Carrick et al. (1962); McConnell et al. (2002)	a, b, c
Adults	30	d		
Forage duration				
Juveniles	45	d		a, b, c
Adults	98	d		
Mid-winter haul-out for juveniles	15	d	Hindell and Burton (1988b)	a, b, c
Resting duration				
Juveniles	2	d		a,b
Adults	1	d		
Diapause	120	d		
Breeding duration	217	d	Laws (1984)	c
Weaning duration	23	d		
Chance of breeding failure for				
>3 year old	0.98			
>4 year old	0.21	-	Fedak et al. (1996); Desprez et al. (2014)	a, b
>5 year old	0.15			
>6 year old	0.75			
Non-energetic pup survival	65.96	%	McMahon et al. (1999, 2000, 2003)	a, eq 3.34

together with the input, determines the behaviour of the system completely.") needed for simulation of the species' life-cycle.

The model follows the scaled DEB-IBM of Martin et al. (2012), with DEB parameters derived from DEBtool (see also section Model modifications, below) using input data—either user defined, or from the DEBtool database 'add_my_pet' (http://www.debtheory.org/). The DEB-IBM includes two entities; individuals (here, seals), and their environment. Individuals are represented using a number of DEB state variables as described in Table 3.1 for more details).

The environment of the individuals is non-spatial and is represented by a set absolute food availability f_{a} (dimensionless, range 0-1.00 representing 0-100% of food availability) which through the included competition term (see section Initialisation, below) becomes the effective food availability f_{eff} (see equation 3.2, and Fig 3.4). Time in the model is represented using finite difference equations for daily time-steps. The value for absolute food availability f_{a} (Table 3.1) was modified from the value of 1.00 derived using DEBtool, as, although this gave accurate results for the remaining DEBtool derived parameters, this value was too high for the DEB-IBM we developed. An absolute food availability of 1.00 assumes that there is unlimited food available, which is not the case for southern elephant seals (as they need to actively forage for their resources). Initial investigations in the model development stage determined that a value of 0.935 was the maximum value of f_{a} that resulted in a stable population. Values higher than this invariably led to an ever increasing population of seals.

While temperature effects in the environment can be crucial to the model responses of some species, southern elephant seals are large, warm blooded, thermoregulating, marine mammals. These homeotherms have a blubber layer that is between 5 and 10cm thick. This gives them a 2°C buffer for changes in temperature, which leaves the effects of temperature changes on metabolism as minimal. The inclusion of temperature effects would certainly be important for poikilotherms, or species such as krill (small invertebrates) who are much more affected by a change in temperature, but this is less important for large mammals whose internal temperature remains stable. Temperature changes are likely to affect food availability in the future. In this model that is encapsulated with the use of food availability terms (f_{a}, f_{eff}).

Process overview and scheduling

Individual variables are updated every time-step, based on sets of finite difference equations. Discrete events, such as birth and death may occur based on the outcomes of these equations. Fig 3.3 describes a single time-step assuming that the initial set-up has already taken place. An independent individual is one that is no longer reliant on its mother (thus excluding

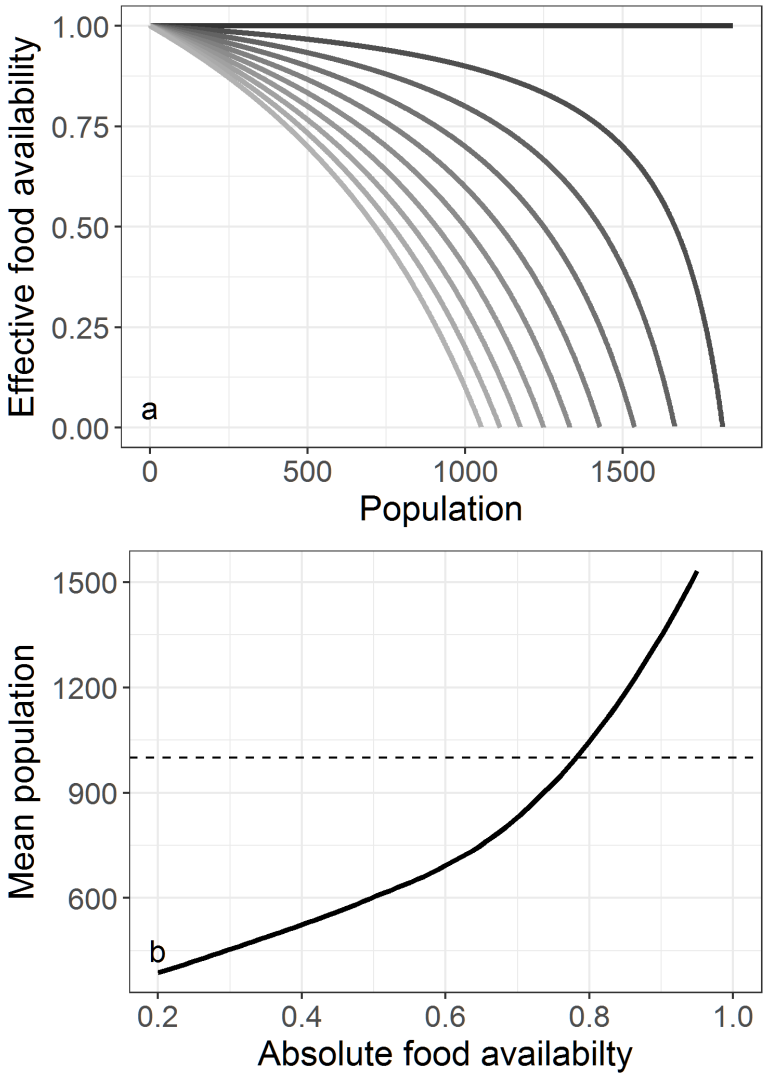

Figure 3.4. Comparison of absolute and effective food availability at a range of population sizes. a) Theoretical effective food availability f_{eff} at different starting levels of f_{a} (range 0.1-1.00 at steps of 0.1: light grey to black) for a range of population P sizes, using equations 3.2 and 3.3 for effective food availability with competition; assuming the individual variability is non-existent (*i.e.* $cv = 0$) and the carrying capacity $K = 1000$. The effective food availability is large for all starting conditions, when there are few individuals within the modelled population. As the population increases, the lower food availability (light grey) is most sensitive to change in population numbers. b) The model maintains a stable population over time, relative to the set f_{a} (0.50-0.95); whereas the population collapses with an absolute food availability <0.50. Dotted line represents the carrying capacity $K =$ 1000 individuals. Total mean of population shows only independent individuals (*i.e.* juveniles and adults) who are impacted by the competition for food (see section Initialisation in section 3.2).

foetuses and pups).

Design concepts

Basic principles The model is adapted from a DEB-IBM for water fleas developed by Martin et al. (2012). DEB theory (Kooijman, 2010b) considers assimilation and energy use of individuals for growth, maintenance and reproduction via a balanced approach for mass and energy (Kooijman, 2010b; Martin et al., 2012). This model thus follows the basic principles of DEB theory as well as IBMs.

Emergence Individual results, and consequent population dynamics, emerge through properties of metabolic organisation (DEB theory) and interaction between individuals (IBM).

Adaptation Adaptive behaviour is not included in the model. Individual variability is applied in the set-up of the model; however, over their lifespan the standard variables remain constant. Consequently the design concepts "Objectives", "Learning", "Prediction", and "Sensing" do not apply in this model. This can change if spatial components are implemented in the model. Additionally "Collectives" are not represented in the model as each individual represents an individual.

Interaction Assumptions are made for interactions during the breeding season which allows females to become pregnant in a model which does not (currently) include males. Indirect interactions are included in the model through a competition formula affecting individual food availability.

Stochasticity Initial stochasticity is included in the model through individual variability iv from the initial parameter settings (see equation 3.1, and section Initialisation, below). Stochasticity is also included in the initialisation of the individuals through a randomly calculated size L within the limits of juvenile (min) and adults (max); through ageing (mortality probability) and non-energetic pup mortality; and breeding sub-models (probability of failed mating at different age classes).

Observation A number of outputs are displayed on the user interface, and each can be exported with ease (see the NetLogo User Manual Wilensky, 1999). In the published model the output includes the overall population trends over time; as well as the population and stage class densities; growth; age at first reproduction and transition to puberty; mean ages, as well as lifespan and mortality causes; fecundity and pup survival. Ultimately, any individual or population based variable can be observed quite easily.

Initialisation

The initialisation of the model uses initial values for all parameters, as listed in Tables 3.1 and 3.2, unless otherwise specified below. The following describes the calculations made to implement individual variability to the model.

Individual variation iv (eq 3.1) is implemented in the model using the parameter cv for energy investment ratio g and effective food availability f_{eff} (eq 3.2), as well as for foraging, moulting, and resting durations. This individual variability is calculated with eq 3.1.

$$iv = e^{(\text{random-normal } 0 \ cv)} \tag{3.1}$$

This creates a log-normally distributed random number with a standard deviation which is user defined. Where "random-normal" is a NetLogo defined variable that reports a normally distributed random floating point number with a mean of 0 and a standard deviation of cv (Wilensky, 1999), (here, 0.05; Table 3.1).

The model includes a population-dependent competition term ΔP (eq 3.3) that directly influences each individual's effective food availability f_{eff} (eq 3.2) through a scaling of the overall food availability term f_{a};

$$f_{\text{eff}} = (f_{\text{a}} + \Delta P)iv \tag{3.2}$$

where

$$\Delta P = (1 - f_{\text{a}})(1 - \frac{P}{2K - P}) \tag{3.3}$$

If the overall food availability f_{a} is set so that the population P is stable, we require ΔP to be positive for a population that is less than the implemented carrying capacity (or expected equilibrium) K, approaching a maximum value of $(1 - f_{\text{a}})$ as P becomes very small (and so effective food availability tends to 1). Once the population grows to a value above K, ΔP turns negative and decreases effective food availability (Fig 3.4a).

The form of ΔP is such that the penalty in effective food availability for increased population increases asymptotically as P approaches a population of $2K$. The whole population is used to determine P and ΔP as dependent individuals (those reliant on their mother) make up $<$10% of the whole population, although only juveniles (including yearlings) and adults are used for analyses of population stability.

The inclusion of a competition term applies self-limitation to the population—if the population is larger than the point where crowding begins to limit the food available for each individual (*i.e.* $P > K$) then the food availability reduces proportionally. Variability in individual fitness and performance is implemented through a random variation in the effective food availability (see eq 3.2).

At the initialisation of the model, the length L (eq 3.4) of each individual is set at a random value between the length at weaning L_x and ultimate length L_m, and is multiplied by the shape coefficient δ_M to convert physical length (in cm) to a dimensionless structural length (see Kooijman, 2010b):

$$L = L_x + \text{random}(L_m - L_x)\ \delta_M \tag{3.4}$$

Initial reserve settings U_E (eq 3.5) are based on the individual's length L (eq 3.4, or structural length L^3), scaled length l (eq 3.6), and energy conductance $\dot{\nu}$

$$U_E = L^3\ \frac{l}{\dot{\nu}} \tag{3.5}$$

where

$$l = \frac{L}{L_{max}} \tag{3.6}$$

and

$$L_{max} = L_m\ \delta_M \tag{3.7}$$

Scaled maturity U_H at the current state and length for initialisation is calculated through dividing the scaled reserve U_E by 2.87. This value is a mean calculated from maturity levels U_H over reserves U_E at lengths for weaning and puberty. This is slightly inaccurate, but only impacts the first individuals that are created in the model; U_E and U_H (as well as U_R) become emergent features for the next generation of individuals (see section Design concepts, above).

Scaled reserve density e (eq 3.8) is calculated for the initialisation of the model, as well as at each time step with calculation of change in reserves. It represents the amount of reserves per unit of structure relative to the maximum amount of reserves per unit of structure (*i.e.* the available energy stored over a period of time, which is particularly important during periods

of fasting (Kooijman, 2010b; Martin et al., 2012)):

$$e = \dot{\nu} \, \frac{U_E}{L^3} \tag{3.8}$$

A sanity check is performed here, to ensure no individuals have maturity levels lower than that of a young juvenile; *i.e.* the current U_H is compared with set threshold levels. These threshold levels (U_H^b, U_H^x and U_H^p, respectively for birth, weaning, and puberty; Table 3.1) represent the threshold values at which an individual transitions to the next stage (foetus, to pup, to juvenile, and ultimately to adult). These are calculated (eq 3.9) from E_H^b, E_H^x and E_H^p as derived from DEBtool, using the surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$ for the scaled model:

$$U_H^b = \frac{E_H^b}{\{\dot{p}_{Am}\}} \tag{3.9}$$

Based on the scaled maturity of the individual, their stage (juvenile or adult), age (between three and 15 years) and hazard rate $\dot{h}$ (eq 3.22; for ageing purposes) are set. Their scaled reproductive buffer U_R is set equal to the scaled maturity (this again is balanced out as an emergent feature over the next generation of seals).

The reproductive threshold U_{cum} (eq 3.10) is included in the model to control the number of births per individual, and is proportional to the individual's size (see section Thresholds for puberty, breeding and death, below). This threshold is modified from Kooijman (2010a, page 38), and considers the cumulative energy requirements for foetal development of southern elephant seals, proportional to the mother's size. This is a function of the energy a mother could acquire based on the absolute food availability; independent of the size of the population."

$$U_{\mathrm{cum}} = \left(L_w^b \; \delta_M\right)^3 \left(\frac{f_{\mathrm{a}} + g}{\dot{\nu}}\right) \left(1 + \frac{3}{4} \, \frac{L_w^b / L_w^m}{f_{\mathrm{a}}}\right) 0.2 \; l \tag{3.10}$$

All remaining settings are set so that none of the individuals are pregnant or have mated, and all individuals are foraging. The model starts on the first of January and uses a run-in period of 50 years to allow for emergent features to come through and improve the stochasticity in the model.

Input data

The model does not use input data to represent time-varying processes. Tables 3.1 and 3.2 summarise the DEB and IBM parameters and the values as they are used in the model.

Sub-models

The following sub-models are implemented for all individuals (unless otherwise specified) that have not died in this time-step. The calculations for changes in energy reserves, maturity, reproductive buffer and growth follow formulations for the scaled model by Martin et al. (2012), which are "algebraically rearranged, reduced (using compound parameters), and scaled with the aim of reducing the amount and types of data needed to parameterize the model for a species". An in-depth guide has been provided by Martin et al. (2012) in their user manual—which is applicable for the following sub-models, unless otherwise specified. Formulations and deviations used in this DEB-IBM for southern elephant seals are provided here.

Update time management The time management sub-model handles the timings of the model. Each time-step represents a single day. At each time-step a day is added to the year as well as to the month, and each individual adds a day to its age. At the end of each month (30 days) the days of the month are reset, and a month is added. When 360 days have passed, the day of the month, day of the year and month of the year are set back to 1 and a year is added to the count.

Reset changes to 0 At each time-step each individuals clears changes set in previous time-steps. Thus dU_E, dU_H, dU_R, and dL (see below) are set to 0.

Calculate reproduction threshold At the start of each time-step the individuals re-calculate their reproductive threshold (eq 3.10), as this is proportional to their size.

Update competition The effective food availability f_{eff} of individuals is updated to include the most recent change in competition, as per equations 3.2 and 3.3.

Check status Each individual has a stage (foetus, pup, juvenile, mature; 0-3, respectively), and a status (mother-dependent, fasting, foraging; 0-2, respectively) which can change, logically, throughout its lifecycle. This sub-model handles the status of each independent individual (*i.e.* those not reliant on their mother).

- Maximum duration of moulting, resting and foraging are set according to their current stage and age.
- Then for the relevant status, a day is added to each 'activity' (foraging, fasting, resting, moulting); if days exceeds the maximum days set for the activity, the activity is changed (*i.e.* from fasting to foraging).
- If the month is December (12) and they are not yearlings (age <360 d), individuals start their annual moulting process.
- If the month is July (7) the juveniles start their annual mid-winter-haul-out.

Check breeding This sub-model handles the breeding process—this, when activated, uses additional sub-models. The breeding checks are processed in reverse-chronological order (from giving birth to impregnation of the mother) so that each action is handled in a subsequent time-step (*i.e.* it is not possible to add a day to a pregnancy and then in the next section already give birth).

a. If the total time of pregnancy has been reached (*i.e.* the time since breeding = total breeding duration + diapause) the individual gives birth. Here settings are altered so that the mother is resting and lactating, but no longer pregnant or impregnated. Here total number of offspring over her lifetime is updated and the age and stage of the offspring are updated.

b. If the mother is 8 days from giving birth (*i.e.* the time since breeding = total breeding duration + diapause - 8 days) her settings are updated so that she comes on to land (status = fasting) in preparation for birth (as per (Laws, 1984; Hindell et al., 1994b; Hindell and Slip, 1997)).

c. If the time since mating equals the species' diapause duration the pregnancy is implemented. The first check is then to make sure that the individual has enough energy to support a foetus through to birth (*i.e.* U_R higher than the reproductive threshold as calculated in equation 3.10). If these energy levels aren't reached, then pregnancy is aborted and the individual continues foraging. If pregnancy occurs: a new offspring is 'hatched'; individual variables are implemented; and the two individuals are connected via their respective IDs.

d. If the individual has been impregnated, or is pregnant, a day is added to her pregnancy.

e. If the individual is breeding but not yet pregnant or impregnated, impregnation happens.

No new individuals are created here as diapause has not yet passed. Rates of successful impregnation depend on the age of the individual (see Table 3.2). So long as they are within a reasonable number of pregnancy attempts (this is set here to a 7 day period), they can try again in the next time-step.

f. If individuals are lactating and have been on land for 19 days (Laws, 1984) they are ready for their next pregnancy. The impregnation sub-model is then implemented.

As the model follows an actual population and lifecycle, the months of year for breeding are important. Offspring are born sometime at the end of September, beginning of October and thus the modelled breeding cycle needs to follow this.

g. If the month is September (9) individuals check that they have enough energy for breeding and that they are old enough for breeding, as above.

h. If all is good – breeding is implemented and the sub-models will be activated in the next time-step.

i. If the month is November (11) and individuals are indicating they can breed, but have so far had no luck they are classified as failed breeders and will return to foraging.

Calculate change in energy reserves dU_E The change in energy reserves is determined by the difference between the scaled mobilization S_C (eq 3.11 or 3.12) and assimilation S_A (eq 3.13 or 3.14) fluxes. The first step in the calculation for change in energy reserves is to ensure that the individual's effective food availability includes the competition term (eq 3.3). If $f_{\text{eff}} > 1$ then f_{eff} is set to 1 as there cannot be more than 100% food availability. The scaled energy reserve e (eq 3.8) is recalculated.

The mobilisation flux S_C (eq 3.11) represents the energy used, following the calculation used by Martin et al. (2012)

$$S_C = L^2 \, \frac{g \, e}{g + e} \left(1 + \frac{L\dot{k}_M}{\dot{v}}\right) \tag{3.11}$$

If the individual is in fasting mode (due to resting or moulting) there is no food intake, and f_{eff} is set to 0; the mobilisation flux (eq 3.12) changes to

$$S_C = \frac{\dot{k}_M \, g \, \kappa}{\dot{v}} \, L^3 \tag{3.12}$$

The assimilation flux S_A (eq 3.13) represents the consumption of food proportional to the

surface area, following the calculation as per Martin et al. (2012)

$$S_A = f_{\text{eff}}\ L^2 \tag{3.13}$$

If the individual is pregnant, up-regulation takes place (Kooijman, 2010b) and the surface area of the foetus L_{foetus} is included in the assimilation flux (S_A; eq 3.14), thus

$$S_A = f_{\text{eff}}\left(L^2 + L_{foetus}^2\right) \tag{3.14}$$

If the individual is a yearling and foraging, an 80% chance is implemented that they are less successful at finding food, and will thus only collect 20% of their otherwise effective food available. The final calculation is for the collection of actual stored energy dU_E (eq 3.15), assuming energy has already been used through the mobilisation flux S_C (eq 3.11 or 3.12),

$$dU_E = S_A - S_C \tag{3.15}$$

Calculate change in maturity dU_H and reproduction buffer dU_R Independent seals need to calculate their change in maturity levels and/or reproduction buffer. Juvenile individuals (with $U_H < U_H^p$) calculate their change in maturity dU_H (eq 3.16):

$$dU_H = (1-\kappa)\ S_C - \dot{k}_J\ U_H \tag{3.16}$$

where $\dot{k}_J\ U_H$ represents the maintenance cost associated with maintaining their current levels of maturity ($\dot{k}_J$ = maturity maintenance rate coefficient). S_C is as per equation 3.11 or 3.12; whichever is relevant to the individual's foraging status.

If individuals have reached the maturity threshold and are considered adults, they calculate the change in their reproductive buffer (eq 3.17). This is calculated as per the change in maturity (eq 3.16), but uses the maximum level of maturity maintenance required by adults U_H^p

$$dU_R = (1-\kappa)S_C - \dot{k}_J\ U_H^p \tag{3.17}$$

Calculate growth dL Growth, or change in structural length (eq 3.18), is calculated for individuals who have not yet reached maximum size (i.e. $L < L_M$)

$$dL = \frac{1}{3}\left(\frac{\dot{v}}{g\ L^2}\ S_C - \dot{k}_M L\right) \tag{3.18}$$

In the case where scaled reserve density e (eq 3.8) falls below the scaled length l (eq 3.6) there is not enough energy to sustain growth (Martin et al., 2012) and dL is set to 0 while the starvation mode is implemented (see eq 3.12). Consequently, energy is diverted from growth to pay for somatic maintenance $\dot{k}_M$ and thus the original calculations for maturity and reproductive buffer (eqs 3.16 and 3.17) are replaced with

$$dU_H = (1-\kappa)S_C - \dot{k}_J\ U_H^p - \kappa L^2(l-e) \tag{3.19}$$

and

$$dU_R = (1-\kappa)S_C - \dot{k}_J\ U_H^p - \kappa L^2(l-e) \tag{3.20}$$

respectively, using the maximum value for U_H (U_H^p) for maintenance allocation for both calculations. As there has been a change in the mobilisation flux S_C (eq 3.12) the scaled energy reserve dU_E is recalculated as per equation 3.15. If the scaled reserve density $e \leq 0$ the individual dies, and links, where relevant, are broken between mother and offspring.

Calculate ageing The ageing sub-model (see Martin et al., 2012; Kooijman, 2010b) is applied to all individuals from the day that they are born and is applied as a deterioration of structure over time using the DEB parameters ageing acceleration $\ddot{q}$; Weibull ageing acceleration $\ddot{h}_a$; and hazard rate $\dot{h}$ Kooijman (2010b). Ageing is assumed to occur due to accumulation of damage inducing compounds proportional to the mobilisation flux S_C. The cumulative scaled acceleration (eq 3.21) and hazard (eq 3.22) rates are calculated for implementation in the ageing sub-model:

$$\ddot{q} = \ddot{q} + d\ddot{q} \tag{3.21}$$

$$\dot{h} = \dot{h} + d\dot{h} \tag{3.22}$$

where $d\ddot{q}$ (eq 3.23), and scaled hazard rate $d\dot{h}$ (eq 3.24), are as per Kooijman (2010b, page 216)

$$d\ddot{q} = \left(\left(\ddot{q}\frac{L^3}{L_M^3}\ S_C + \ddot{h}_a\right)e\left(\frac{\dot{v}}{L}\right) - \dot{r}\ddot{q}\right) \tag{3.23}$$

$$d\dot{h} = \ddot{q} - \dot{r}\dot{h} \tag{3.24}$$

where $\dot{r}$ (eq 3.25) is the rate of growth

$$\dot{r} = \frac{3}{L} dL \tag{3.25}$$

Update changes For female southern elephant seals breeding can start at the age of three, whereas somatic growth continues until the age of six (Desprez et al., 2014). The calculations for dU_R (eq 3.20) are, however, only carried out for adults and thus remain at 0 for individuals who are yet to reach maturity. To accommodate for allocation of energy to reproduction while the individual is yet to reach maturity, for these individuals dU_H is split on a 60: 40 ratio between dU_R and dU_H (based on trials during the model development stage).

As all the calculations have been carried out, changes for dU_E, dU_H, dU_R, and dL need to be implemented through the simple addition of $U_E = U_E + dU_E$; and the same for the remaining changes. Where the accumulated U_H of juveniles exceeds their transition limit U_H^p the remainder of dU_H is transferred to their reproductive buffer U_R.

Yearlings have a lower survival rate than older individuals (which is related to their fitness and experience/success at foraging, as well as their mother's fitness; *e.g.* McMahon et al., 1999). To implement this in the model, an additional energetic related mortality check is added where if $U_H < 0.92 \times U_H^x$ the yearling dies. A sanity check is implemented here to ensure that individuals, whose energy levels have fallen below 0, die. This check also ensures that if a mother dies during a pregnancy, the foetus also dies. Connections are terminated if a mother or pup dies during the weaning stage, and the relevant variables are updated for the mother (or pup) who survives. In the unlikely circumstance that a mother dies while lactating, the pup goes into fasting mode until completion of the moulting period (∼50 days; Table 3.2).

If juvenile seals have reached puberty ($U_H \geq U_H^p$) they transition to adult stage. Changes from foetus to pup are handled in the breeding sub-model; changes from pup to juvenile are handled in the update offspring energy sub-model.

Update offspring energy The updating of offspring (foetus) energy is applied from a mother's position. As the foetus is immobile, there is no mobilization flux used in any calculations, and the energy reserves are assumed equal to that of the mother (Kooijman, 2010a).The first step is to update the foetus' growth (eq 3.26)

$$L = L + r_B L_M \tag{3.26}$$

using the von Bertalanffy growth rate r_B (eq 3.27)

$$r_B = \frac{\dot{v}}{0.545\ L_M} \tag{3.27}$$

which has been modified from the originally published $r_B = \dot{v}/(3\ f_{\text{eff}}\ L_M)$ Kooijman (2010a), as when using the original equation, pregnancies lasted for 900 days and pups were too large (see section Model modifications, below). This is followed by the calculation for scaled energy reserves (eq 3.28)

$$dU_E = e_{\text{mother}}\ L^2\ \kappa_F \tag{3.28}$$

where the scaled energy reserves of the mother e_{mother} are used for the calculation of energy uptake from food, proportional to the foetus' surface area and the increased assimilation capabilities κ_F. In case of foetal development, all energy reserves are used to reach maturity and thus the scaled maturity equals the scaled energy reserves, thus $dU_H = dU_E$. The changes are then implemented following the simple addition of $U_H = U_H + dU_H$ for U_H and U_E. The mother's reproductive buffer U_R is updated through the removal of the energy allocated to the foetus

$$U_R = U_R - (dU_{E\ \text{foetus}}\ \kappa_F) \tag{3.29}$$

Update pup energy A sanity check is performed to ensure the pup has a mother, following which the calculation for scaled energy reserve dU_E is as per equation 3.15, where the assimilation flux S_A changes (eq 3.30)

$$S_A = \frac{f_{\text{eff}} L^2}{\kappa_L} \tag{3.30}$$

The effective food availability f_{eff} is set to $2 \times f_{\text{a}}$, and κ_L is implemented to allow for the increased 'fattiness' of southern elephant seal milk (up to 55%; see Hindell et al., 1994a) as well as the increased allocation efficiency of milk. The mobilisation flux S_C for pups (eq 3.31) becomes

$$S_C = 3\left(L^2 \frac{g\ e}{g+e}\left(1 + \frac{L\dot{k}_M}{\dot{v}}\right)\right) \tag{3.31}$$

Calculations for scaled maturity U_H are as per eq 3.16, and $dU_R = 0$. The change in growth dL of pups (eq 3.32) is modified from eq 3.18 to account for the increased growth rates of

southern elephant seals during weaning

$$dL = \frac{\dot{v}}{g\ L^2}\ S_C - \dot{k}_M L \tag{3.32}$$

The calculated changes are applied to the pup, and the energy allocated by the mother are removed from her reproductive buffer (eq 3.33)

$$U_R = U_R - (S_{A\ \text{foetus}}\ \kappa_L) \tag{3.33}$$

During the weaning period, the mother tracks the time that she has been lactating. Once this period exceeds the individual's weaning duration, the link between mother and pup is broken, and the pup's status is updated to juvenile. The pup remains on land for a moulting period while the mother returns to foraging.

Apply aging The ageing previously calculated is now applied to the scaled hazard rate $\dot{h}$ (equation 3.22) through a randomly selected range between 0 and a user-defined mortality variable (mortality-float) multiplied by the individual's individual variability (equation 3.1). If the individual variability is less than 0.95, the mortality chance is increased to account for the lesser overall fitness of the individual. If the mortality value is less than the hazard rate $\dot{h}$, the individual dies and any links with offspring or mother are severed, unless the mother is pregnant when she dies—then the foetus also dies.

Non energetic pup mortality is also dealt with here for pups and yearlings. If a randomly selected value (between 0 and 1) is less than the value set for the pup mortality (see Table 3.2), the pup or yearling dies. The pup-mort parameter is set at a user defined variable ranging between the minimum and maximum observed pup mortality; following data collected by several authors (*e.g.* McMahon et al., 1999, 2000, 2003) from Macquarie Island. The pup mortality (eq 3.34) is converted from annual chance of survival to daily chance of mortality using the scaling:

$$\text{daily-pup-mort} = \frac{1}{360}\ \left(1 - \frac{x}{100}\right) \tag{3.34}$$

where x is the annual chance of survival (as a percentage) from the non-energetic pup survival as presented in Table 3.2).

Stop commands There are three stop commands applied to the model which are implemented when the model's run time has passed the set time that the model is set to run (in years); when the population has collapsed (i.e. there are less than 20 individuals left in the

model), and; when the population has exceeded 50 times the starting population (assuming a starting population of 250, this becomes 12,500), thus reducing computational limitations.

Final update The final update for the model includes collecting the final information from individuals who died in this time-step—as this information is needed for collection of results (maximum age, size and number of offspring). Once this last set of data has been stored, the output is updated according to user defined requirements (*e.g.* total count, population dynamics, fecundity of females, length of individuals, etc.).

Remove dead individuals The individuals who died in previous sub-models are now removed from the model. This is done as the final step so that all the information gained in the time-step can be collected before 'dead' individuals are removed from the model.

Model modifications

We adopted the scaled version of the standard DEB model following Martin et al. (2012), meaning that the model was simplified as the state variables for *reserves* E_E, *maturity* E_H, and the *reproduction buffer* E_R are divided by the maximum surface-area-specific assimilation rate $\{\dot{p}_{Am}\}$. This removes the units of energy from the model (Kooijman et al., 2008; Martin et al., 2012). This allows the use of scaled reserve U_E, scaled maturity U_H, and scaled reproduction buffer U_R, as well as scaled life-stage transition parameters (threshold values) for birth U_H^b, weaning U_H^x, and puberty U_H^p; see Table 3.1.

Competition

The DEB-IBM for southern elephant seals is not spatially resolved. As such it cannot explicitly model the effects of overcrowding leading to increased competition for food and greater metabolic costs of longer foraging trips. To account for these limitations the model includes a population-dependent competition term ΔP (eq 3.3) that directly influences each individual's effective food availability f_{eff} through a scaling of the overall food availability term f_{a} (eq 3.2) as explained in section Initialisation, above.

Foetus and pup development

Calculations for foetal and pup growth (eqs 3.26—3.33; section Sub-models, above) are based on Kooijman (2010b), but have been modified for this model, following Kooijman

(2010a) and Roberts (2014). These modifications take into account the expected length and weight of pups at birth (110 cm and 45 kg) and weaning (125 cm and 117 kg; *e.g.* McMahon et al., 2000, 2017; Clausius et al., 2017b), as well as pregnancy and weaning durations (217 and 23 days, respectively; Laws, 1984).

Although predicted weights and sizes from an initial model were similar to those observed for pups at Macquarie Island, both the pregnancy and weaning durations were too high in the model. Foetal growth in the model was too slow when using the original equation (von Bertalanffy growth rate); pregnancies lasted around 900 days (expected 217 days Laws, 1984). To resolve this we adjusted the equation for foetal growth (equation 3.27) by reducing the impact that ultimate size and the mother's effective food availability f_{eff} have on the growth rate. We also included the increased assimilation capabilities of the foetus κ_F to the energy transferred from the mother (equations 3.28 and 3.29).

As the weaning duration in the model (269 days) was too high (expected 23 days Laws (1984)) we modified the equations for the pups' energy intake and growth (equations 3.30—3.33, section Sub-models; Update offspring energy). These changes take into account the short weaning period of southern elephant seals, the extreme weight gain of pups ($\sim$70 kg between birth and weaning), and the extreme fattiness of southern elephant seal milk (up to 55% toward the end of weaning Hindell et al., 1994a). The species used for the development of these original equations by Roberts (2014) were the tammar wallaby *Macropus eugenii* and echidna *Tachyglossus aculeatus*. The fat content in the milk for these species is much lower than that of the southern elephant seal; around 4% and 31%, respectively (Meurant, 1995). To account for this, we added a pup assimilation factor κ_L to equations 3.30 (for calculations of the scaled energy reserve dU_E and mobilisation flux S_A) and 3.33 (the mothers' reproductive energy dU_R expenditure) to increase the pups' energy intake.

To take into account the increased energy mobilisation of pups we modified equation 3.31 by increasing the mobilisation flux S_C by a factor of three, compared to the original implementation of the equation for foraging independent individuals (eq 3.11). The outcome of this equation is implemented in the calculation for physical growth dL (eq 3.32) where the physical growth of pups is tripled (compared to the original calculation, eq 3.18) to ensure that the changes in growth are proportional to the changes in energy storage.

Yearling mortality

During the first 12 months, southern elephant seals have a higher mortality than for the rest of their life (McMahon and Burton, 2005). This is implemented in the model using two different methods; one for energetic mortality (starvation), and one for non-energetic mortality (*e.g.* predation by orcas *Orcina orca*).

Energetic mortality generally affects the yearlings soon after weaning as they are left on the beach by their mothers. In the first 4-5 weeks the yearlings go through starvation mode, after which they leave the island for the first time to forage. The pup mortality is larger for smaller seals (annual chances of survival vary between 71.6% for weaners heavier than 135 kg, to 54.2% for those weighing less than 95 kg; McMahon et al., 2000). Although no conclusive data is available, it is expected that of the approximate 35% of yearlings that die, around 80% die of starvation, and 20% of non-energetic factors (Hindell, pers comm 2017). To account for this we have implemented a modified survival threshold in the model for yearlings, which is sensitive to reductions in stored energy. After initial results from model runs during development this threshold was set at 92% of their weaning threshold (which is directly linked to their mass). Additionally (see section Sub-models, above) a reduced chance of successful foraging has been implemented for yearlings, to account for their foraging naïvity.

Non-energetic mortality is presented in the model through a mortality parameter. The parameter is a user defined value between the minimum and maximum of observed yearling mortality, following data collected from Macquarie Island (*e.g.* McMahon et al., 1999, 2000, 2003) and converted from annual chance of survival (field observations) to daily chance of mortality (modelled; see equation 3.34). The combination of the two mortalities balances out to the expected yearling survival rate.

Thresholds for puberty, breeding and death

The transition threshold from juvenile to adult stage U_H^p has been changed from the DEBtool value to reduce the time it takes for an individual to become an adult. Using the original value, individuals transitioned to adult stage at around 15 years of age as opposed to the expected age of six (Desprez et al., 2014).

As the population structure and projections in initial model development were particularly sensitive to changes in the reproductive buffer U_R of mothers, a breeding threshold U_{cum} was included in the model to set a minimum energy level at which individuals could sustain a

pregnancy (eq 3.10). The inclusion of the breeding threshold allows for the exclusion of males in the DEB-IBM. This is validated based on the assumption that the population trajectory of southern elephant seals is only weakly dependent on male numbers (as explained in the introduction, as although there is a 1:1 ratio of females to males at birth, males make up only 36% of the adult population of which only ∼8% contribute to the next generation). Thus we added a breeding threshold U_{cum} which reduced the overall fecundity to near half of the observed fecundity in the field (up to 0.5 for female births by females McMahon et al., 2005b), and reduced the number of births over a lifetime below the expected breeding success (13 pups per lifetime Desprez et al., 2018).

The reproductive buffer U_R contains the stores of energy solely for reproductive purposes (as opposed to maintenance and maturity). This buffer becomes depleted when a mother is pregnant, and particularly while she is lactating (as, during the final 30 days while she is on land, she does not take in any energy). The stored energy increases again following the pre- and post- moult foraging trips. If the stored energy exceeds the reproductive buffer U_{cum}, the mother (if successfully impregnated) initiates her pregnancy after the diapause; if not then she aborts the pregnancy and skips that year of breeding. Thus, as the buffer is increased, it becomes more difficult to have consecutive pregnancies, particularly as mothers can lose up to 35% of their mass during lactation (Fedak et al., 1996). If the buffer is lower, more female seals are born and the population increases; when the buffer is set too low (below the cumulative cost of raising a pup) too many would-be mothers die during pregnancy, causing the population to collapse. At levels that were too high, too few pups were born as mothers chose not to breed, and again the population collapsed. The threshold (eq 3.10) is scaled to the size of the mother, as smaller mothers have less energy to allocate to foetal development McMahon et al. (2017).

During the model development stage, the sub-model for ageing was insufficient; individuals well exceeded their expected maximum age of 23 years. Consequently, a mortality parameter was included in combination with the DEB parameters to control the lifespan of individuals (see section Sub-models, above).

Model evaluation and sensitivity analyses

The aim of the model evaluation was to determine the abilities and limitations of the model. For the southern elephant seal DEB-IBM this included i) being able to reproduce life histories as emergent model features, ii) being able to use the model to project a stable population

over time, and iii) having realistic population dynamics and structure based on emergent life history features (such as age at first breeding, lifespan, fecundity and (yearling) survival).

We ran sensitivity analyses to test the limits of the model and to get a better understanding of the results the model might produce. The model we have built contains a large number of parameters, many of these are derived using DEBtool (see section Entities, state variables, and scales in section 3.2, and Table 3.1, above) to ensure correct growth rates and energy intake and expenditure for the selected species. Of the remaining parameters those related to well observed characteristics of the species (such as life history traits and breeding behaviour) were not altered. For the sensitivity analyses we chose to focus on those parameters that directly influence the individual's energy intake (absolute food availability f_a), and the required levels of stored energy for maintenance and maturity at which an individual transitions to the next stage of their life (transition thresholds at birth U_H^b, weaning U_H^x, and puberty U_H^p; Table 3.3). These thresholds are directly linked to each individual's size and weight and therefore the levels at which these transition thresholds are set are expected to affect the lifetime success of the individual (and consequently of the population as a whole). The high (95%) and low (55%) values for the sensitivity analyses for (absolute) food availability were chosen to represent extreme scenarios for resource availability that either makes the population grow excessively, or causes a near collapse of the population. The 10% change to the transition thresholds were chosen as indicative change representing our uncertainty in the parameters as these thresholds, specifically, represent the required size of the individuals at selected life stages (whereas other DEBtool derived parameters are used for the underlying mechanics).

Given that we are using DEBtool for determining parameter values, using a greater than 10% variation of those DEB values takes us away from the theory of DEBtool; thus larger increases in the variation would discount theoretically derived values based on well tested general methods of DEB theory Kooijman (2010b). For example, the threshold for puberty U_H^p was previously reduced in the model development stage (see section Thresholds for puberty, breeding and death in section 3.2, above) by close to 20% of the original value to match the complex life histories of southern elephant seals, indicating that changes of more than 10% could be unrealistic. We compared results of 10 Monte Carlo simulations of the sensitivity runs and analysed the results of 100 year simulations (after the run in period). Statistical analyses were done in *R* (R Core Team, 2017, version 3.4.1) using two sided t-tests with a 99% confidence interval. The t-test is calculated using a sample size of 10, where each sample size is calculated as the mean of the 100 year run. The stable model, with the standard parameters is hereafter referred to as the 'baseline model'.

Table 3.3. Parameter values used for baseline model and sensitivity analyses for changes in absolute food availability f_{a} and transition thresholds for weaning E_H^x, and puberty E_H^p. Low and high variations for transition thresholds vary by 10% of the baseline value. '—' indicates value is as per baseline model (*i.e.* no change).

	f_{a}	E_H^x	E_H^p
Baseline	0.935	6.5×10^7	1.45×10^8
f_{a} low	0.55	—	—
f_{a} high	0.95	—	—
E_H^x low	—	5.85×10^7	—
E_H^x high	—	7.15×10^7	—
E_H^p low	—	—	1.305×10^8
E_H^p high	—	—	1.595×10^8

3.3 Results

Baseline model

The baseline model (set with standard parameters as described in Tables 3.1, 3.2 and 3.3) produced populations that were stable over long periods of time (exceeding 2000 years). Fig 3.5 shows a mean stable population of independent (those not reliant on their mothers; *i.e.* juveniles and adults) seals, at 1464 individuals ($\pm$11, within a range of 1191-1553) over 100 years (from 10 simulations).

The population structure in the model is an emergent feature determined by the breeding success and survival of individuals. In the baseline model, these dynamics remained stable over time with the greatest proportion of the population being juveniles (Fig 3.6). Juveniles (excluding yearlings) and adults, annually, make up 49.83$\pm$0.71% and 39.51$\pm$0.74% of the population, respectively. Pup and yearling survival also remained stable over time at 97.55$\pm$0.36% and 65.76$\pm$2.17%, respectively (Table 3.4; columns 2 and 3 compare published observations with baseline model results for selected properties). The age structure and cumulative survival of the modelled population in comparison to observational data is further discussed in Chapter 4.

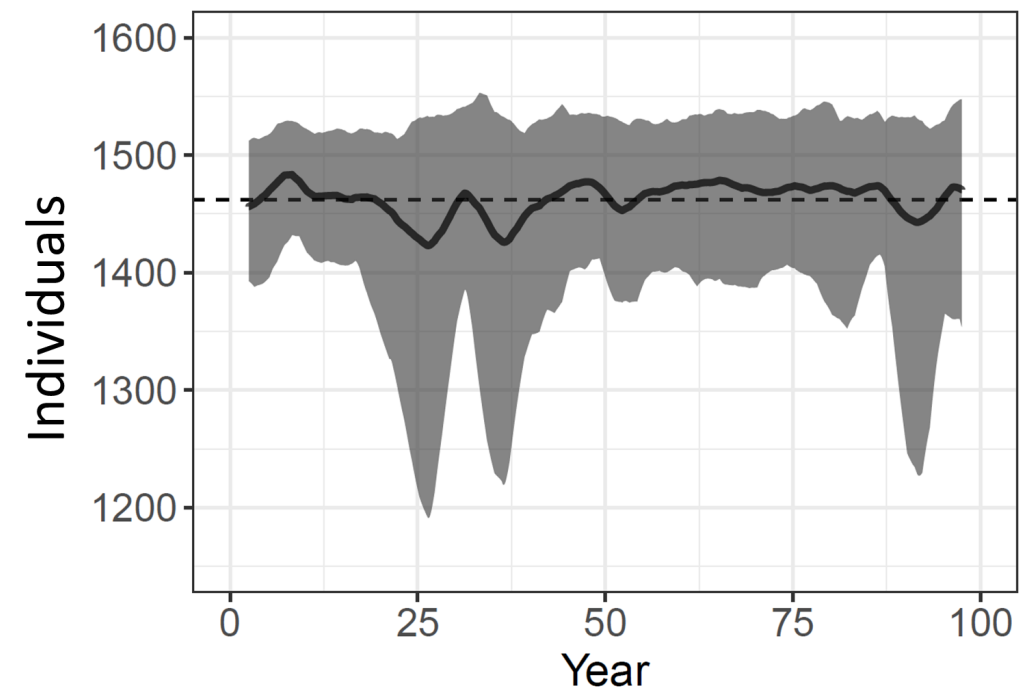

Figure 3.5. Baseline population showing 5-year running mean of 10 simulations over 100 years (excluding the run-in period), and overall population mean, at an absolute food availability $f_{\mathrm{a}} = 0.935$. The population remained stable at a mean of 1464±11 individuals (range 1191-1553). The grey enveloping the mean (black line) represents the minimum and maximum number of individuals in the population at each time step. The total mean population shows only independent individuals (*i.e.* juveniles and adults), as per Fig 3.4.

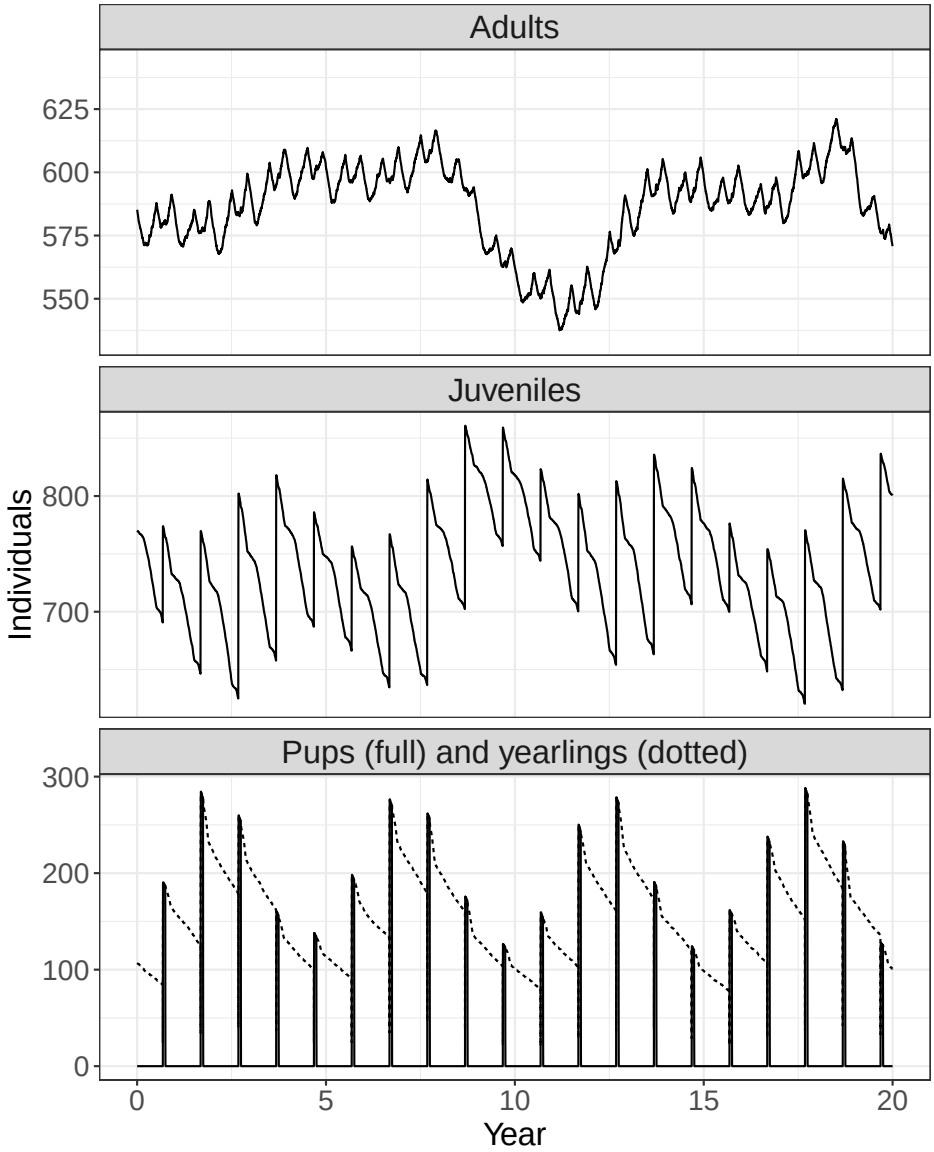

Figure 3.6. Population dynamics in the baseline model; mean of 10 runs, over 20 years. Individual stages as per transition thresholds, except juveniles do not include those under 1 year old — these are represented as yearlings in the third panel. The 'Pups, and yearlings' panel shows the survival at different stages (see also Table 3.4). Transition stages for adult: $U_H \geq U_H^p$, juvenile: $U_H^x \leq U_H < U_H^p$, pup: $U_H^b \leq U_H < U_H^x$. Note different scales on y-axis.

Table 3.4. Means (±standard deviation) from Monte Carlo simulations ($n = 10$ over 100 years) for baseline model and sensitivity analyses. Grey cells indicate significant differences between means of baseline model and simulation runs (t-test; $p < 0.01$). The changes applied to the model parameters are described in Table 3.3. * Indicates the distribution of selected model results are presented in Fig 3.7; ** indicates the distribution of selected model results are presented in Fig 3.8, and; *** indicates that the distribution of selected model result is presented in Fig 3.9. Results for lifespan of individuals exclude deaths of yearlings, and proportion of juveniles excludes counts of yearlings. Effective food availability is averaged for individuals with age >360 d. [a] Females counted in 2015; modelled population is smaller to limit computational costs (see section 3.4). [b] Indicates a significant difference in model results, although t-test failed as data has a reported variability of 0.00 (see also section Life history and breeding traits in section 3.3).

			Food availability		Weaning threshold		Puberty threshold	
	Observed data	**Baseline model**	**Low**	**High**	**Low**	**High**	**Low**	**High**
Population size **	2740[1] [a]	**1464±11**	425±2	1501±10	1470±12	1275±1	1474±33	1452±3
Juvenile proportion **	–	**49.83±0.71%**	60.1±0.20%	48±0.80%	55.6±0.50%	33±0.17%	31.1±0.75	72.6±0.78%
Adult proportion **	–	**39.51±0.74%**	29.7±0.19%	41.2±0.76%	33.3±0.57%	55.6±0.20%	58.1±0.97%	16.8±0.73%
Pup survival **	95% [2]	**97.55±0.36%**	96.2±1.37%	97.6±0.48%	97.6±0.38%	97.6±0.29%	97.6±0.35%	97.3±0.45%
Yearling survival *	54.2%-71.6%[3]	**65.76±2.17%**	43.2±2.92%	66.3±3.56%	73.5±1.04%	40±2.95%	59.8±3.12%	68.1±1.30%
Min reprod. age (yr)	3 [4]	**4.40±0.00**	5.40±0.00 [b]	4.40±0.00	4.40±0.00	4.40±0.00	4.40±0.00	4.40±0.00
Generation time (yr) **	7.9-11.3 [5, 6]	**9.49±0.03**	11.48±0.00	9.52±0.05	9.59±0.07	9.46±0.00	9.48±0.02	9.47±0.00
Juvenile age (yr) *	–	**3.85±0.07**	4.58±0.01	3.57±0.10	4.13±0.07	2.57±0.00	2.36±0.02	5.5±0.08
Min adult age (yr) **	6 [4, 7]	**5.11±0.04**	8.88±0.04	5.01±0.02	5.18±0.03	4.66±0.02	3.97±0.02	6.49±0.05
Adult age (yr) *	–	**10.74±0.06**	13.80±0.04	10.47±0.08	10.50±0.15	10.23±0.03	9.43±0.19	12.10±0.08
Lifespan (yr) *	10-14 [8, 9]	**11.73±0.08**	12.88±0.07	11.49±0.08	11.09±0.14	12.20±0.07	11.67±0.27	11.76±0.06
Max lifespan (yr) ***	23 [10]	**28.80±0.99**	30.42±0.99	28.72±1.18	27.87±1.04	30.04±1.04	28.27±1.05	29.43±1.21
Fecundity *	0-0.5[5]	**0.28±0.00**	0.35±0.00	0.28±0.00	0.28±0.00	0.39±0.00	0.31±0.01	0.26±0.00
Max pups per mum **	13[11]	**8.90±1.10**	12.2±1.23	9.00±0.67	8.50±0.71	14.1±0.99	9.60±0.97	8.70±0.82
Juvenile size (cm) *	150-240 [12]	**168±0.16**	163±0.02	167±0.23	169±0.18	163±0.04	159±0.06	174±0.22
Adult size (cm) *	275 [13]	**188±0.31**	194±0.13	190±0.31	188±0.27	197±0.05	185±0.80	191±0.22
Max size (cm) *	280 [14, 15]	**193±0.59**	215±1.30	200±2.75	197±1.17	210±0.04	195±4.81	199±0.68
Effective food**	–	**0.71±0.00**	0.88±0.00	0.71±0.00	0.71±0.00	0.82±0.00	0.68±0.02	0.74±0.00

References: [1] Hindell et al. (2017) ; [2] Hindell and Burton (1987) ;[3] McMahon et al. (2000);[4] Laws (1956);[5]McMahon et al. (2005b);
[6] Desprez (2015);[7] Desprez et al. (2014);[8] Carrick et al. (1962);[9] Hindell (1991); [10] Hindell and Burton (1988b);
[11] Desprez et al. (2018); [12] Boyd et al. (1994); [13] Bell et al. (2005); [14]Laws (1953); [15] McLaren (1993).

The mean age at first successful breeding in the baseline model is at four years old (Table 3.4), with a generation time of 9.5±0.03 years (see section Life history and breeding traits in section 3.3). First attempts at breeding are around the age of three; however the individuals generally have not reached the appropriate energy storage threshold to maintain these early pregnancies. The modelled individuals successfully reproduce up to 11 times within their lifetime, but often no more than nine. The mean fecundity (reproductive rate; *i.e.* number of female offspring per year McMahon et al. (2005b)) of the population is 0.28 (range 0-1; Table 3.4), which is as expected considering the inclusion of the reproductive threshold U_{cum} to account for only female births in the model.

Individuals transition to adult stage at just over five years of age, with a mean lifespan of 11.73±0.08 years. The mean ages of juveniles and adults are 3.85±0.07, and 10.74±0.06 years, respectively. The mean maximum lifespan (from the absolute maximum ages reached by individuals in the model) sits at 28.80±0.99 years (see section Lifespan and mortality in section 3.4). These estimates exclude the deaths of yearlings. The maximum size reached by individuals is 193±0.59 cm, with a mean of 168±0.16 cm and 188±0.31 cm for juveniles and adults, respectively (Table 3.4).

Sensitivity analyses

Results for sensitivity analyses for changes in absolute food availability and transition thresholds at weaning and puberty are presented in Table 3.4. For ease of understating the scale and direction of change for the different parameters the results are visualised in Figs 3.7 and 3.8. Exceptions are made for the minimum reproductive age, which had little to no variation between results, and maximum lifespan which is presented in Fig 3.9.

Changes in absolute food availability

Monte Carlo simulations indicated that mean population numbers were significantly different from the baseline model. Changes to the resource availability resulted in a mean population of 425±2 and 1501±10 individuals, respectively (Welch two sample t-test: $p < 0.01$, $n = 10$; Table 3.4, Fig 3.8a) for a decrease (55%) and an increase (95%) of the absolute food availability f_{a}.

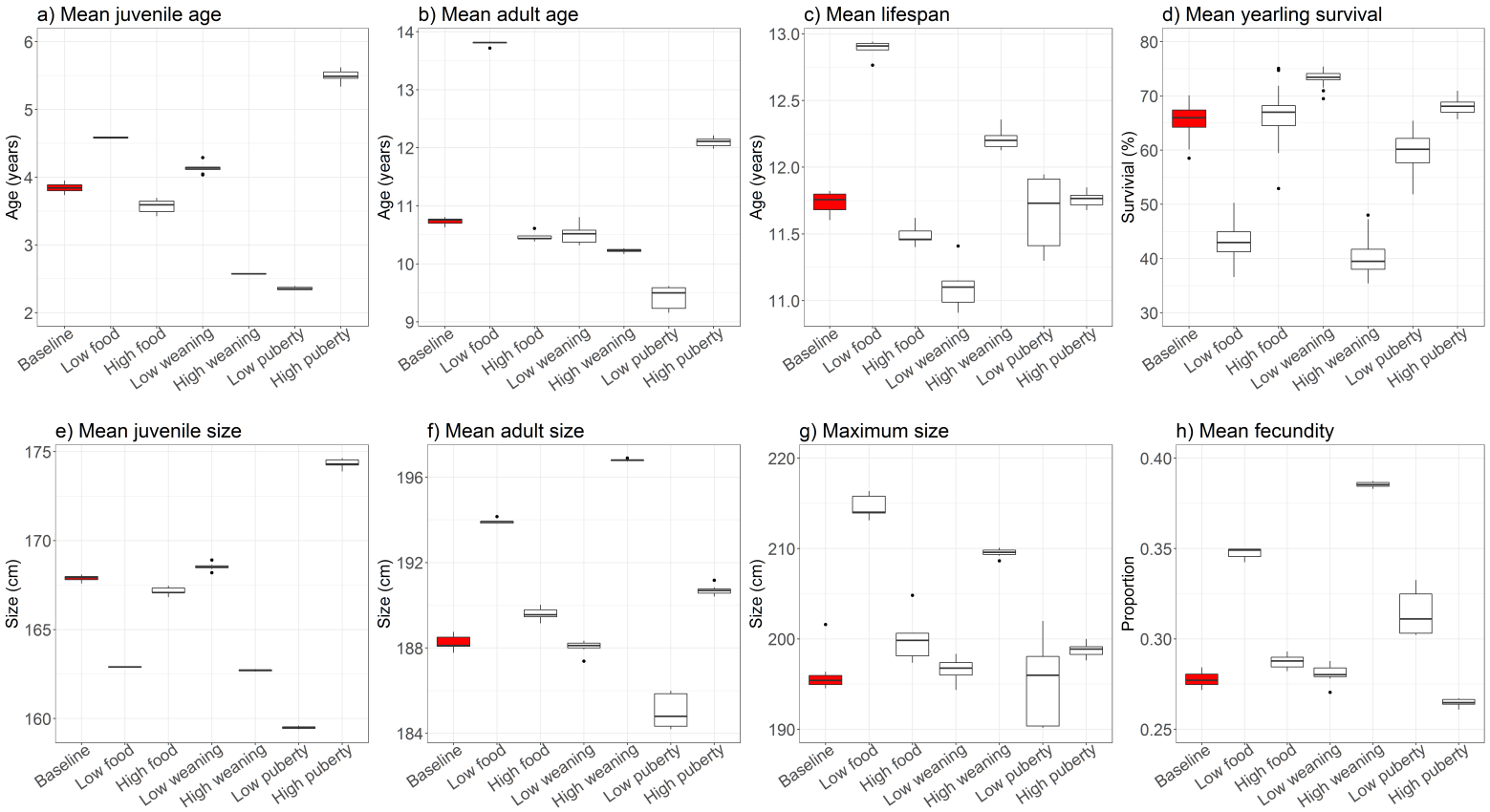

Figure 3.7. Comparison of results from Monte Carlo simulations (means of $n = 10$, over 100 years), showing a) mean juvenile age, b) mean adult age, c) mean lifespan, d) mean yearling survival, e) mean juvenile size, f) mean adult size, g) maximum size, and h) mean fecundity of females in the baseline model and sensitivity runs. For each sub-plot the baseline result is highlighted in red. Results for means±standard deviation are found in Table 4.

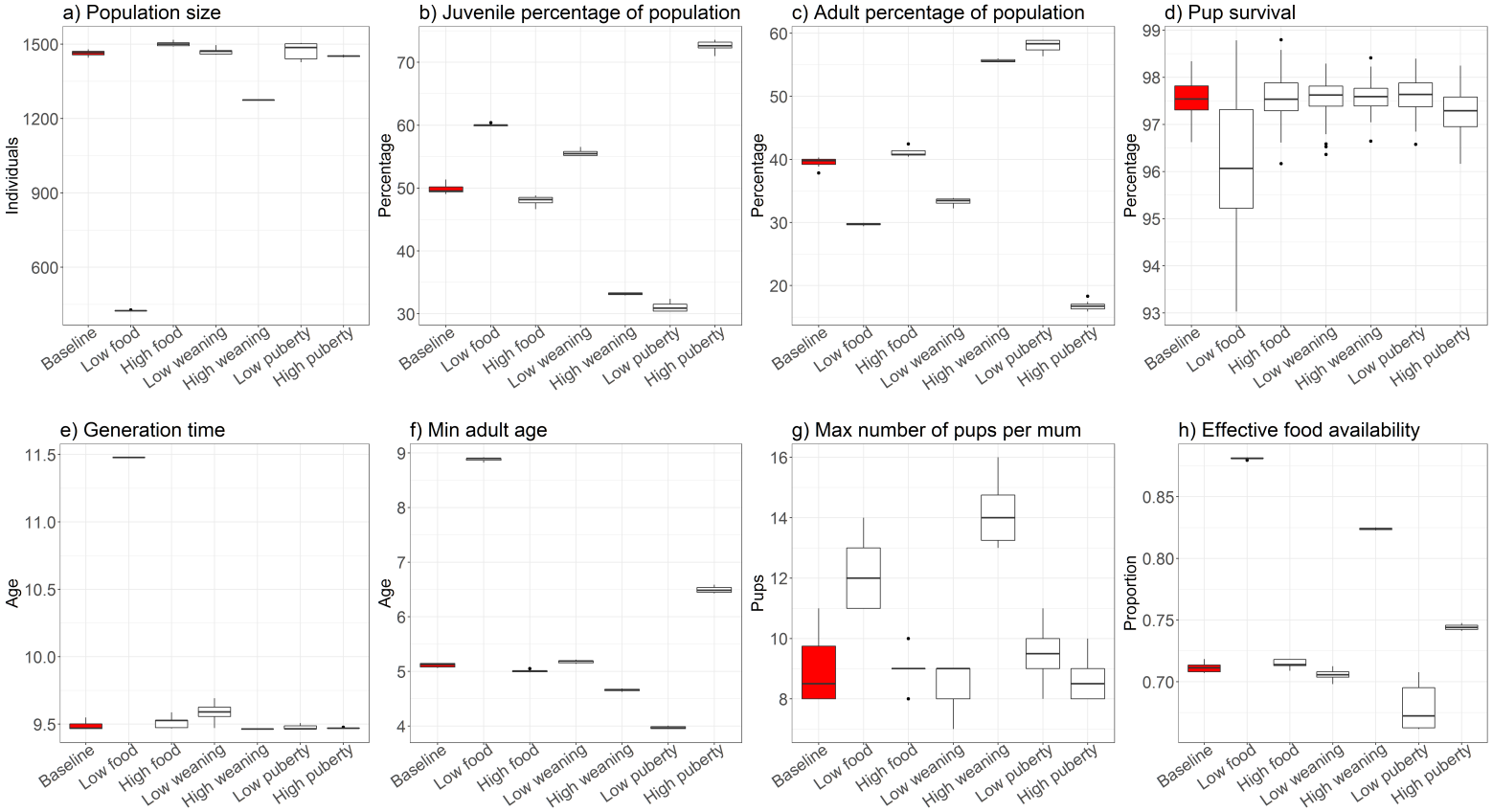

Figure 3.8. Comparison of results from Monte Carlo simulations (means of $n = 10$, over 100 years), showing a) population size, b) juvenile percentage of population, c) adult percentage of population, d) pup survival, e) generation time, f) minimum adult (transition) age, g) maximum number of pups per mum, and h) effective food availability in the baseline model and sensitivity runs. For each sub-plot the baseline result is highlighted in red. Results for means±standard deviation are found in Table 4.

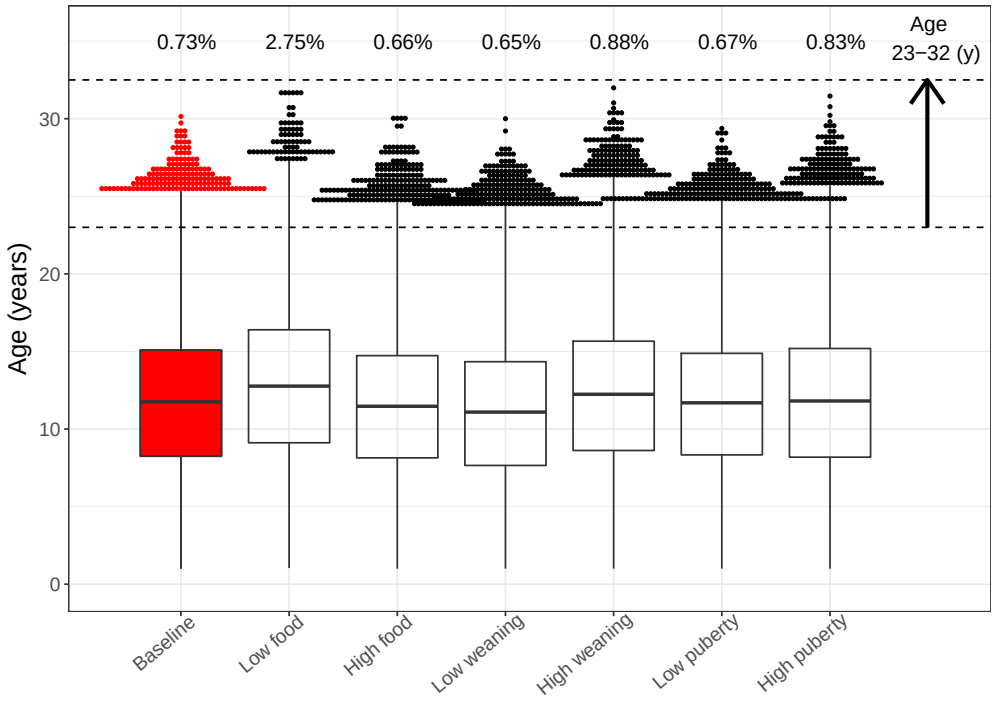

Figure 3.9. Population-level distribution of lifespan of individuals in the baseline and sensitivity model runs (100 years x 360 days x 10 runs). Outliers consist of ages 1.5 $\times$ the interquartile range, above the upper quartile. Individuals reaching ages >23 (the maximum recorded age in the field Hindell and Burton (1988b)) made up 0.73% in the baseline model (red; n = 107808); 2.75% and 0.66% with low and high absolute food availability (n = 31488 and 110790, respectively); 0.65% and 0.88% with low and high weaning threshold (n = 10466 and 105817, respectively); and 0.67% and 0.83% with a low and high puberty threshold (n = 108412 and 107416, respectively). Deaths of yearlings have been removed from the analyses, and the baseline result is highlighted in red.

At a lower absolute food availability the proportion of adults and juveniles in the population changed significantly; >60% of the population are juveniles, and <30% adults (Fig 3.8b, c). Yearling survival dramatically reduced (to 43.2±2.92%; Fig 3.7d) as the fecundity increased (0.35±0.00; Fig 3.7h) and mothers gave birth to up to 14 pups in their reproductive lifespan (Fig 3.8g). The mean age of juveniles and adults, as well as their mean lifespan (Fig 3.7a-c), increased and individuals took a year longer to become sexually reproductive (at 5.40±0.0 years old; Table 3.4). Juveniles transitioned to adults significantly later (at 8.88±0.04 years; Fig 3.8f) and individuals survived to almost 32 years of age (Fig 3.9). The mean juvenile size, however, reduced, which is in contrast to the mean adult and maximum sizes, which

increased. The maximum size reached was 215±1.3 cm (Table 3.4, Fig 3.7e-g).

At a higher absolute food availability ($f_{\mathrm{a}} = 0.95$) there was no change (Table 3.4) in the age at which individuals become sexually reproductive, nor was there a significant change in the proportion of juveniles (Fig 3.8b), the fecundity (Fig 3.7h), or yearling survival rates (Fig 3.7d). Although there were significant differences in the mean age and size of juveniles and adults, as well as for the age of transition to adult stage, and the proportion of adults in the population (Table 3.4), these differences were smaller than for a lower absolute food availability (Fig 3.7a, b, e, f, Fig 3.8c, f).

Changes in weaning threshold

A decrease in the weaning threshold E_H^x significantly changed the population structure and dynamics (Table 3.4), with a greater proportion of the population being juveniles than adults (55.6±0.50% and 33.3±0.57%; Fig 3.8b, c), and a significant increase in the survival rate of yearlings (73.5±1.04%; Fig 3.7d), although there was no significant change in the mean population size (1470±12 individuals; Fig 3.8a). Monte Carlo simulations indicated significant increases in the mean ages and lifespan of individuals (Table 3.4), with the increase in mean juvenile age and decrease in mean lifespan being the most prominent (Fig 3.7a, c). There were no significant changes in the mean fecundity (Fig 3.7h) or maximum number of pups per mother (Fig 3.8g), and only juveniles showed a significant difference in the mean size (Fig 3.7e), compared to the baseline model.

A higher weaning threshold resulted in a significant reduction of the population size (1275±1; Fig 3.8a) as well as a significant reduction in the survival of yearlings (40±2.95%; Fig 3.7d), changing the dynamics to a population with 33±0.17% juveniles and >55% adults (Table 3.4; Fig 3.8b, c). Although there was no change in the minimum reproductive age, the mean adult and juvenile ages significantly reduced; juveniles transitioned to adult stage sooner (Fig 3.8f); and the lifespan and maximum ages increased (Fig 3.9). Fecundity also rose significantly (Fig 3.7h), and the mean number of pups produced by each mother increased to 14.1±0.99 (Table 3.4; Fig 3.8g). The mean juvenile size was significantly smaller than in the baseline model, however the mean adult and maximum sizes were significantly larger (Table 3.4, Fig 3.7e-g).

Changes in puberty threshold

The mean population was not significantly different for either a decrease or an increase in the puberty threshold E_H^p, at 1474±33 and 1452±3 individuals, respectively (Table 3.4; Fig 3.8a). The population structure and dynamics, however, changed significantly. At a lower puberty threshold a significantly lower proportion of yearlings survived their first year (59.8±3.12%; Fig 3.7d), and the juvenile proportion of the population was 31.1±0.75%; with adults making up 58.1±0.97% of the population (Fig 3.8b, c). The age at transition to adult stage was more than a year lower than in the baseline model (Fig 3.8f); this is reflected in the mean juvenile and adult ages (Table 3.4, Fig 3.7a, b). The mean and maximum lifespan, however were not significantly different (Fig 3.7c, Fig 3.9). There was no significant difference in the maximum size reached, however the mean juvenile size was lower, and the mean adult size higher, than those found in the baseline model (Table 3.4, Fig 3.7e-g).

There were significant changes in the population dynamics following an increase in the puberty threshold, with an increase in the yearling survival rate (to 68.1±1.30%; Fig 3.7d) and a large increase in the juvenile proportion of the population (72.6±0.78%, compared to only 16.8±0.73% adults Fig 3.8b, c; Table 3.4). Additionally the age of transition (Fig 3.8f), as well as the mean juvenile and adult ages, increased significantly (Fig 3.7a, b). There was no significant change in the mean or maximum lifespan. The fecundity was significantly reduced (Fig 3.7h), although there was no significant difference in the maximum number of pups produced by each mother (Table 3.4; Fig 3.8g). The mean juvenile and adult sizes were significantly larger than the baseline results, although there was no significant difference in the maximum size reached (Table 3.4, Fig 3.7e-g).

The maximum and absolute maximum lifespan from both the baseline model and the sensitivity analyses (Table 3.4) are higher than those observed in the field (23 years old Hindell and Burton, 1988b), <1% of the population in the baseline model reached a maximum age >23. In the simulation runs this ranges from 0.65-2.75% of the modelled population, overall (Fig 3.9).

3.4 Discussion

The southern elephant seal DEB-IBM that we developed successfully replicated the general life-history and population behaviour of seals at Macquarie Island, while taking into account female births only. The model also illustrated how changes in food supply mediated through

the size of pups at weaning affects population growth rates with positive rates associated with high weaning masses, and *vice versa*. This is important because for the first time we present information showing how environmental change is linked to individual animal performance; how performance affects vital rates (survival and fecundity), and; how changes in vital rates are manifested at the population level. We find that population growth rates are most sensitive to changes in survival rather than changes in fecundity, as might be expected for long-lived multiparous animals that place a higher premium on their own survival rather than that of their offspring (Eberhardt, 2002).

The main goal of the project was to develop the first DEB-IBM for higher trophic-level species with complex life histories and to be able to simulate the energetic requirements of complex top predators in order to quantify how changes in the environment affect population growth rates and structure. We focused on female southern elephant seals as they have been part of extensive longitudinal studies on Macquarie Island, and census data on their life history and breeding traits are readily available. The ability to quantify prey consumption by predators is an essential component in ecosystem based management; as such a model that takes this as well as behavioural traits into account during the full year becomes a useful tool for management and conservation purposes. Our model shows that it is possible to have detailed energetics as well as behavioural traits included for higher trophic-level species in ecosystem models, through combining dynamic energy budget theory and individual-based modelling.

The sensitivity analyses were undertaken with changes to three model parameters. The changes to the weaning and puberty thresholds (the levels at which individuals are weaned, and physically become adults, respectively) were set at a 10% decrease and increase from the baseline (the standard parameter settings). Changes to the food availability parameter were made so that the lower limit (55% of available food) was set to represent an extreme scenario under which there was just over half the available food as is presented in the baseline model. The upper limit was set at 95% available food, as tests with an unlimited food supply were unfeasible as the model didn't stabilise, predominantly due to computational limitations. These limitations were also the deciding factor regarding the set carrying capacity (or expected equilibrium) K of the model; at a stable population between 800-1600 individuals the model could be run overnight, and results can be compared to existing populations. For analyses of larger populations, we recommend a simple change to the model to include collectives, or super-individuals (*sensu* Scheffer et al., 1995), where one super-individual comprises multiple individuals, to limit computational costs.

Life history and breeding traits

Life history traits (age at first reproduction, age at stage transition, maximum age, growth, and fecundity) are emergent behaviours in our model. The results of the baseline model are comparable with observations on Macquarie Island (see Table 3.4, and Figs 3.7 and 3.8), suggesting our model is successfully reproducing the behaviour of southern elephant seals. The behaviour, survival and breeding success of individuals ultimately affects the overall population structure and population trajectory.

Breeding

Females in the baseline model become adults around five to six years of age, and start reproducing around the age of four. This aligns with published data on ages at which individuals become sexually active and to which they undergo somatic growth (Laws, 1956; Desprez et al., 2014). The generation time in the model is approximately 9.5 years; compared to 11.3 and 7.9 years previously estimated (respectively; McMahon et al., 2005b; Desprez, 2015); where generation time is defined as the mean age of mothers at first birth (Lebreton, 2005). Note that the observed minimum age at first successful reproduction has a reported variability of 0.00 (Table 3.4). This is as the analyses were undertaken on the means of the minimum age of each model run. Thus there were 10 means of the minimums, and considering that southern elephant seals have a short period during which they actually breed (at the same time every year) the mean minimum ages were identical.

The breeding behaviour of modelled individuals is mainly dependent on their stored reproductive buffer. If their accumulated reproductive buffer falls below the minimum breeding threshold, pregnant individuals will prioritise their own survival and abort their pregnancies; affecting their overall fecundity. Additional controls on reproduction are set through a chance of successful breeding that is dependent on age (*i.e.* a higher chance of reproductive success at four and five years (Fedak et al., 1996; Desprez et al., 2014); see Table 3.2). From conception through to weaning a pup's energy intake is dependent on the mother's energy stores (Fedak et al., 1996; Arnbom et al., 1997; McMahon et al., 2017). This emphasises the importance of maternal foraging success (McMahon et al., 2005a) as up-regulation of energy intake during pregnancy is essential for mothers to be able to carry the offspring through to birth and weaning (Kooijman, 2010b). Consequently, a fitter mother will produce a bigger pup with a better chance of surviving to breeding age. In the field it is not unusual to observe seals that do not breed for a year, or at all (Fedak et al., 1996). Small females

may abort before reaching full term, or may not get pregnant (Laws, 1984; Hindell et al., 1994b; Fedak et al., 1996; McMahon et al., 2017). The duration of the lactation period in the current model is set at 23 days, following observations on Macquarie Island. In future implementations of this model the duration could be implemented in the model as an emergent property based on the energy stored by the pups. This implementation would require a simple single-line change in the code for future versions at the 'give-birth' section.

Fecundity (or the reproductive rate) of southern elephant seals at Macquarie Island has previously been estimated to vary between 0 and 0.5 (McMahon et al., 2005b), indicating that not all seals breed every year. The emergent mean fecundity of each model simulation falls within that estimate (at 0.28), while taking into account female births only. The lowest resulting fecundity was seen in simulations of the model with a higher puberty threshold (at 0.26), and the highest fecundity was seen with a lower weaning threshold (at 0.39). This is a logical result as for simulations with a higher puberty threshold, individuals need to allocate more energy stores to their own growth and thus have less energy to allocate to breeding. The opposite is true for a lower weaning threshold, considering less energy needs to be allocated to personal growth while the pups are weaning. Consequently some of the energy gains may be allocated to the reproductive buffer sooner, resulting in an overall higher allocation of energy for breeding. This is reflected in the changes seen in the number of pups produced by these individuals in the model (10 and 16 pups, respectively) over their reproductive lifespan.

Ages at transition

Changes to the parameters for absolute food availability and the transition threshold for weaning and puberty affected the emergent life history traits. A reduction of the available food affected the age at first reproduction (as described above); individuals started breeding later. This is not surprising considering a reduction in food means a reduction in energy intake, which therefore means it will take longer to reach energy related thresholds. Under scenarios with a lower absolute food availability or a high puberty threshold, the age at which individuals transition from juvenile to adult stage (*i.e.* when they reach physical maturity) also occurs considerably later in life (at 8.88 ± 0.04 and 6.49 ± 0.05 years, respectively). This increase in the transition age is reflected in the higher mean juvenile and adult ages (Fig 3.7a, b).

Simulations with a higher absolute food availability, an increase in the weaning threshold, and a decrease in the puberty threshold had no effect on the age at first breeding, but

did have significant effects on the ages at which individuals became adults. Particularly simulations with a high weaning or low puberty threshold reduced the age at transition (to 4.66±0.02 and 3.97±0.02 years, respectively). This is explained by the different allocation of energy storage for physical maturation U_E and the reproductive buffer U_R where the energy allocated to reproduction is not affected by changes in the transition thresholds, thus the age at first breeding does not change. With a reduced puberty threshold, the individuals became physically mature before they became sexually reproductive.

Pup and yearling survival

The mean annual pup survival in the baseline model (taking into account the combined energetic and non-energetic mortality for pups and yearlings) is 97.55±0.63% for pups (while with their mother) and 65.76±2.17% for yearlings after weaning (Table 3.4, Fig 3.7d). No records are published on the survival rates of pups during the lactation period, however, it is estimated that approximately 5% die during this period (Hindell and Burton, 1987), due to being squashed by either their mother, or other adults on the beach. This is not explicitly included in the model, but emerges from the non-energetic mortality factor applied to pups and yearlings.

The yearling survival rate lies within the size dependent range observed for yearlings at Macquarie Island (54.2% to 71.6%; McMahon et al., 2000). The survival rate of yearlings varied significantly between the sensitivity runs of the model (ranging from 40±2.95% to 73.5±1.04%, respectively, for a higher and lower weaning threshold). These extremes are reasonable considering the energetic mortality threshold of yearlings is closely related to their weaning threshold (see section Sub-models; Update, in section 3.2, above) and while this is changed in the model, there is no change implemented to the energy intake in the same period. Consequently yearlings in the model where there is an increase in the weaning threshold may not be able to sustain these high energy levels, and die. Those individuals who do survive through to sexual maturity, are more successful at breeding (indicated by the highest fecundity rate; see above) reflecting the observed survival differences between small and large pups on Macquarie Island (*e.g.* McMahon et al. (2000)).

Lifespan and mortality

There were no significant differences in the maximum lifespan of individuals in the sensitivity runs, compared to the baseline (although a lifespan of close to 2 years longer for a lower

absolute food availability, and an increase in the weaning threshold gave a p-value of 0.028 and 0.014, respectively). The maximum lifespan of individuals in the model is higher than the maximum ages observed on Macquarie Island, however, the percentage of individuals with higher ages was low (range of 0.65-2.75% between simulations; Fig 3.9). As initial tests of the model showed that these few animals in the older age classes contribute very little to the overall population parameters, we made the decision not to add an absolute maximum age to the model at which individuals were forced to die, but for the maximum age to remain an emergent feature.

Changes in the puberty threshold did not change the mean lifespan of individuals, whereas both changes in the absolute food availability and the weaning threshold did. The mean lifespan of individuals increased for a higher weaning threshold, as well as with lower absolute food availability, as did the maximum and absolute maximum lifespan in these scenarios. This is not unreasonable when looking at research on effects of calorie restriction on lifespan of a range of species, although opinions vary (Heilbronn and Ravussin, 2003; Sohal and Forster, 2014). This calorific constraint at a lower absolute food availability would be an oscillating occurrence, parallel to the variations in population size, and consequent effective food availability (see section Population size and dynamics, below).

Individual growth

The maximum size that individuals reached in the baseline model, as well as for each of the sensitivity runs, is lower than the field observations at Macquarie Island (195-215 cm; Table 3.4, and 280 cm; Table 3.1, respectively), although the modelled mean juvenile size sits within the predicted range (150-240 cm Boyd et al., 1994)). The lower size is likely to be due to changes made to the transition threshold for puberty in the model development stage to account for a more realistic age at which individuals reach physical maturity and become adults (see section Thresholds for puberty, breeding and death in section 3.2). In simulations with a lower puberty threshold, the individuals had a lower mean and maximum size than the baseline (Fig 3.7e-g), thus following the same trends as the changes observed in the baseline, compared with field observations (*i.e.* lower sizes for a lower puberty threshold). This is particularly clear in the differences for mean juvenile size (Fig 3.7e), and can be related back to the younger age at which these individuals become adults (Figs 3.7b, and 3.8f), and *vice versa* for an increase to the puberty threshold.

An increase in the food availability resulted in larger adults compared to the baseline model,

and a decrease in the available food also resulted in significantly larger adults (Fig 3.7f, g), although juveniles in both simulations remained smaller than in the baseline model (Fig 3.7e). This may be explained by the changes in the effective food availability, which increased at smaller populations—consequently producing individuals who (while not under periods of calorific constraint; see section Population size and dynamics, below) would grow faster and larger than their counterparts.

Population size and dynamics

The number of individuals at which the population stabilises is partially dependent on the competition term ΔP (equation 3.3); this implements self-limitation to the population and maintains a stable, density regulated population, as is observed on Macquarie Island (de Little et al., 2007). The competition takes into account the carrying capacity (or expected equilibrium) K, the current population P, and the absolute food availability f_{a}. A stable population is maintained at an effective food availability f_{eff} somewhere between 0.75-0.9. There is variability in the modelled population caused by changes in the effective food availability, as individuals enter and leave the population. This fluctuation has also been observed in the field, and is thought to be related to the effects of climate variability at foraging grounds and the consequent changes in food availability observed three years prior (van den Hoff et al., 2014).

3.5 Conclusion and next steps

The DEB-IBM we developed for southern elephant seals produced a biologically realistic, stable population, where individuals reproduce at the expected age, finish somatic growth (reach physical maturity) after reaching sexual maturity and reach the observed life expectancy (based on expectations from the Macquarie Island population). The model can be used as a stand-alone, single species model for projecting effects of intrinsic and extrinsic changes on individuals and the population through analyses of behaviour and energy use. The model is developed in such a way that, with relative ease, it could be implemented for other seal species, or a range of other marine mammals or birds.

Our model is not spatially resolved, and as such we do not have a prey-field. Instead, we have a value for absolute food availability f_{a} (currently set at 0.935). The exclusion of males makes little difference in this case, as the absolute food availability can be simply adjusted

to produce a stable population with either just females or males and females. To make the model more realistic, the currently used relative (analytical) food availability could be modified so that more realistic prey fields are included in the model (see (*e.g.* Martin et al., 2012; Pethybridge et al., 2013)). If we develop a spatially explicit version of this model then the presence of males becomes more important as their different foraging patterns may impact food availability differently. Including a more realistic prey field, and making the model spatially explicit, would also include adding prey dependent energy densities, improving the accuracy of the predator's energy intake and use at different times and locations. A detailed sensitivity analysis is recommended for development of a spatially explicit DEB-IBM for southern elephant seals, as energetic intake and requirements may change (particularly with implementation of actual foraging behaviour). This may alter the results to some extent, based on the sensitivity of this model to changes in resource availability and transition thresholds.

Future development of this model could include explicitly modelling male births in the model and, when the model is spatially explicit, modelling the southern elephant seal population in its entirety. This would involve lowering the energetic cost of birth to ensure mothers produce a 1:1 ratio of female and male pups, and increase fecundity closer to 0.5. However, including explicit representation of males will make the entire model more complex considering they have different foraging patterns, different energetic costs associated with different growth, age of physical and sexual maturity, as well as different mortality rates (as explained in section 3.1). Consequently the simplest solution to having male births included in the model, without increasing the complexity too much, would be to remove males after weaning. This would ensure that the mother's energy expenditure on births will be more accurate than in the current model, however complexity in the model, regarding different life histories of males and females, will be limited. The only time we should consider it is if we have a spatially explicit prey-field.

Further modifications to the model could allow DEB-IBMs to be coupled with end-to-end ecosystem models to improve the representation of top predators through inclusion of detailed behavioural traits as well as energetic requirements. As such it could be used to infer management decisions for relevant fisheries, or for ecosystem management. As it stands now, we show that the complex life histories of southern elephant seals can be represented using DEB-IBMs. This model can project population dynamics which can be used to obtain a better understanding of potential drivers behind changes in populations.

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Data Availability Statement: The southern elephant seal DEB-IBM output is publicly available from the IMAS data portal (http://dx.doi.org/10.4226/77/5ab1cc3f83ca4), and a commented version of the model is publicly available from the NetLogo Modelling Commons: DEB-IBM for southern elephant seals (http://modelingcommons.org/browse/one_model/5348).

Chapter 4

Using the DEB-IBM to assess the drivers of the decreasing population of elephant seals at Macquarie Island

Abstract

Southern elephant seals are predatory, capital breeding, marine mammals with a circumpolar distribution. The population on Macquarie Island has been a part of longitudinal studies since 1949 and is in decline at an average rate of -1.46% per year. The exact drivers behind the population decline are unknown, and while migration has been discounted, competing hypotheses postulate increase in female mortality, decrease in recruitment, breeding success, environmental changes at foraging grounds and yearling survival. Our aim was to investigate if a DEB-IBM can be used to evaluate four hypotheses regarding the observed population decline on Macquarie Island through implementing scenarios of i) climate variability ii) reduction of yearling survival iii) reduction in the fecundity of mothers, and iv) density dependence in the model. The modelled population trajectory for all scenarios (except a reduction in fecundity of mothers) closely followed the observed trend in the decline of southern elephant seals at Macquarie Island. The climate scenario showed that yearling survival was particularly affected by resource availability. Survival rates ranged from 30% to 70% depending on the severity of the climate event. The scenario for yearling survival created unrealistic transition ages between sexual and physical maturity stages and also affected the fecundity of mothers (allowing them to have more consecutive pregnancies). The population trajectory of the fecundity scenario did not follow the observed trend at Macquarie Island. This simulation showed that the cost of reproduction at a young age is high, and consequently more pregnancies occurred for older mothers. In the density dependence scenario, the population

trajectory closely matched that of Macquarie Island. The underlying emergent properties of the population and individuals were reasonably realistic. An overall weakness in the model was a poor representation of interannual variability, as compared to the observations. Thus, although the model produced interesting emergent behaviour of individuals and the overall population, none of the scenarios in isolation could explain the driver behind the observed population decline. We conclude that it is likely that a combination of drivers has resulted in population change at Macquarie Island.

4.1 Introduction

Apex predators provide an integrated signal of the health status of the environment and tracking their numbers provides an indication of how this changes over time. The longer life span of apex predators such as seabirds and marine mammals results in slower responses to changes in their environment, resulting in long-term trends (Hindell et al., 2003; Thompson et al., 2012) meaning that they are well suited to informing us of long term-trends in the environment, rather short term variability, such as seasonal patterns. Being aware of the changes in population status and trends of these higher trophic level predator species, particularly of those that are affected by current and ongoing changes in the global environment, can tell us a lot about the state of the environment, and ecosystem structure and function (Hindell et al., 2016). This is particularly the case in the Southern Ocean, a region which has major influences on the global climate (see *e.g.* Constable et al., 2014), and where direct observations are difficult and expensive.

There is increasing evidence that the Southern Ocean is changing (Constable et al., 2014) which not only has an effect across species but also within species (*e.g.* Raymond et al., 2014; Reisinger et al., 2018). The physical changes either seen or expected in the future include (but are not limited to) changes in sea surface temperature and sea ice extent (Smetacek and Nicol, 2005), as well as changes to frontal systems and mixed layer depths (Sallée et al., 2010; Constable et al., 2014). These changes directly affect lower trophic levels, which flows on to higher trophic levels, as these species are influenced directly by the abundance and distribution of prey (Reisinger et al., 2018). The Southern Ocean is home to a multitude of apex predators including the southern elephant seal *Mirounga leonina*.

The southern elephant seal has been the focal species of longitudinal and temporal studies (McMahon et al., 2005a,b; Hindell et al., 2016; Reisinger et al., 2018) as it is a large predatory marine mammal with a circumpolar distribution which makes it a good study

species in the Southern Ocean. There are four genetically distinct sub-populations, of which only the population at Macquarie Island is in decline (McMahon et al., 2005a; van den Hoff et al., 2014; Hindell et al., 2016, 2017). These seals were commercially harvested for their blubber from the early 19th to early 20th century (see Hindell and Burton, 1988a). The population may since have surpassed their pre-exploitation numbers (*e.g.* Hindell and Burton, 1987; Hindell, 1991; McMahon et al., 2005a). This increase in the population may have also increased the competition for resources, potentially straining the population. Although the decline of the southern elephant seal population at Macquarie Island are unlikely due to a population overshoot, the hypotheses surrounding this is yet to be rejected outright (McMahon et al., 2005a). The latest counts estimate population size of 76 000 individuals in 2001 (McMahon et al., 2005a), and down to 60 298 individuals a decade later (van den Hoff et al., 2014; Hindell et al., 2016). Thus in the period post-exploitation, from 1949-2015, the southern elephant seal population at Macquarie Island has virtually halved (Hindell et al., 2017).

Hypotheses on the population decline at Macquarie Island

The drivers of the decline at Macquarie Island are unknown, and while emigration has been discounted (van den Hoff et al., 2007), there are competing hypotheses (*e.g.* McMahon et al., 2005a). An increase in female mortality, combined with a decrease in recruitment, which may be related to environmental changes at foraging grounds (van den Hoff et al., 2014), is one potential driver of a declining southern elephant seal population at Macquarie Island. As the southern elephant seal population at Macquarie Island is density-regulated it incurs high levels of competition for food when carrying capacity is reached (McMahon and Burton, 2005; de Little et al., 2007). Environmental changes such as changes in sea ice extent, interannual variability of the position of oceanic frontal zones and productivity, and climatic events (McMahon and Burton, 2005; van den Hoff et al., 2014) may reduce carrying capacity (Biuw et al., 2007). While these changes affect the environment of the southern elephant seals, the physical changes to large, warm blooded, thermoregulating, marine mammals are negligible. These mammals are highly insulated and thus their metabolism and growth responses are not directly affected by these changes (as was explained in more detail in Chapter 3).

Another hypothesis concerns pup and yearling survival (McMahon et al., 2003). First year survival rates of southern elephant seals are influenced by their size and condition at weaning (McMahon et al., 2000); the survival of pups may be related to the condition of their mother (Hindell et al., 1994b; McMahon et al., 2017). Additionally, post weaning survival may also

be related to prey availability (McMahon and Burton, 2005); yearlings forage in different grounds than older juveniles. This may create a segregation between age classes and is thought to help avoid intra-specific competition (Field et al., 2005).

Breeding success is thought to be a potential driver for population decline (Authier et al., 2012), although a long-term population decline is not thought to affect the age at first breeding (Desprez et al., 2014). While breeding success of female southern elephant seals is dependent on age (Fedak et al., 1996; Desprez et al., 2014) there is no observed female breeding senescence (Hindell, 1988). Female southern elephant seals can start breeding at the age of three, with highest success at the age of four or five (Laws, 1956; Desprez et al., 2014). Fecundity for southern elephant seals (number of female offspring per year) sits between 0 and 0.5 (McMahon et al., 2005a; Desprez et al., 2018). To preserve their own chances of survival some female seals may choose not to breed every year (Hindell et al., 1994b; Fedak et al., 1996; McMahon et al., 2017); the mother can lose around 35% of her mass while lactating (Hindell and Slip, 1997; Desprez et al., 2014).

Quantitative testing of competing hypotheses

To test the effect of different hypotheses on the population, and through this process, to explore whether we can rule in (or out) any of the hypotheses as a likely driver of the population decline we quantitatively test the competing hypotheses using a DEB-IBM (see Goedegebuure et al., 2018, presented in Chapter 3 of this thesis). A DEB-IBM is an individual-based model (IBM; Grimm et al., 2005; Railsback and Grimm, 2011) that is coupled with dynamic energy budget (DEB; Kooijman, 2010b; Sousa et al., 2010) theory to allow for modelling life histories, behaviour, and energy use of individuals (Martin et al., 2012; Goedegebuure et al., 2018). We have previously demonstrated (Goedegebuure et al., 2018) that the DEB-IBM for southern elephant seals can be used to depict emergent model features such as breeding, pup survival, as well as behavioural traits and that the model can project a stable population using parameter settings as presented in published data on the breeding and life history traits of southern elephant seals from Macquarie Island (Goedegebuure et al., 2018). The DEB-IBM allows us to implement different scenarios and track the behaviour and emergent properties of individuals over >10 generations of southern elephant seals. Comparing the emergent properties with observations from Macquarie Island can help us identify what hypothesis may, or may not, be the driver behind the observed population decline.

Here we aim to quantitatively test the competing hypotheses, regarding the potential drivers

of the observed population decline in southern elephant seals at Macquarie Island, by implementing scenarios for i) climate variability ii) reduction of yearling survival iii) reduction in the fecundity of mothers, and iv) density dependence, in the DEB-IBM of Goedegebuure et al. (2018). To evaluate the performance of the model, we analysed the long-term effects of changes on the population (see section 4.2), through sensitivity analyses of emergent life history traits, population growth rates, and breeding success (Bailleul et al., 2007; Caswell, 2001; Kight et al., 2012; New et al., 2014). We try to answer three questions to analyse the fit and match of the model to the observations from Macquarie Island: i) Can the results from the hypotheses reproduce the exponential decline as observed on Macquarie Island? ii) How well does the emergent change in the population dynamics match the Macquarie Island data?, and iii) Is the change in population projection from the modelled data realistic given the changes in emergent individual behaviour and population dynamics?

4.2 Methods

The DEB-IBM we use has been described in detail in the previous chapter. Here we outline the essential components and refer the reader to the previous chapter if more detail is required. This DEB-IBM combines the stochasticity of IBMs and the deterministic components of DEB theory, to model individual southern elephant seals during four life stages (foetus, pup, juvenile or adult). The population is controlled through effective food availability applied to individuals, while accounting for intraspecific competition. To test each of the hypotheses, some modifications were made to the baseline model presented in Chapter 3 to allow for implementation of the scenarios. These modifications and the effects of those changes on the model are described below.

For all hypotheses the implementation of the scenario is set at 20 years after the run-in period (*i.e.* at year 70), which, when the timeline is adjusted to match the observations on Macquarie Island, starts around 1940, and continues for the remainder of the model run. The modifications for the model are all implemented at the 'time management step' in the model (see Figure 3 in Goedegebuure et al., 2018), with modified equations added to their respective sections in the model code.

Hypothesis 1 - Climate variability

The foraging grounds of southern elephant seals, near frontal zones, eddies, or the Antarctic ice edge, are affected by climatic variability which influence the oceanic fronts and sea ice extent (see McMahon et al., 2005a; Crocker et al., 2006, and references therein). The widespread biological effects of physical changes in the environment remain largely unknown, although it is widely accepted that these physical changes are reflected in population parameters of top predators (Croxall et al., 1992; Vergani et al., 2001; Crocker et al., 2006) as climate variability can cause interannual variation in resource availability (McMahon et al., 2005a; van den Hoff et al., 2014; Clausius et al., 2017a).

One such regular occurring climatic event that can cause interannual climate variation in resource availability is the El Niño Southern Oscillation (ENSO). During El Niño there is a marked warming of sea surface temperatures which may cause reductions in food for predators (Crocker et al., 2006). On the other hand, a La Niña event is accompanied by a decrease in sea surface temperatures, and can cause an increase of food availability in foraging grounds (Vergani et al., 2001; Crocker et al., 2006). Another is the Southern Annular Mode (SAM), which characterises the strength of the polar vortex through changes in polar anomalies which alter pressure, wind strength, primary production, sea surface temperatures, and sea ice growth (van den Hoff et al., 2014; Clausius et al., 2017a; IPCC, 2007; Lefebvre et al., 2004). During periods with a positive SAM there is a negative anomaly in the atmospheric pressure at higher latitudes and weakening of sub-polar westerly winds. This stimulates plankton production due to nutrient upwelling and cooling of sea surface temperatures. The opposite is true for periods of negative SAM. Seasonal anomalies in SAM also affect the sea ice growth; a positive tendency in SAM leads to strengthening winds over the continent as the westerlies contract poleward. Due to the presence of the Amundsen Low this leads to increased sea ice in the Ross Sea and decreased sea ice in the Bellingshausen and Amundsen Seas. The opposite is true during a negative SAM (IPCC, 2007; van den Hoff et al., 2014). Although the overall trend has been positive in the last decades, there is variation in the degree and strength of the SAM anomalies (see Marshall, 2018; IPCC, 2007).

To test if the model could match the observed decline in the southern elephant seal population at Macquarie Island, we test the varying role of ENSO and SAM cycles on the assumed food availability of individuals. We do this through including a sinusoidal change in the effective food availability of individuals. Throughout this chapter this is referred to as the climate variability scenario. Essentially SAM displays a roughly three to five-year cycle (Marshall, 2003), and ENSO a roughly three to seven-year cycle (Trenberth et al., 2007). We choose to

implement the sinusoidal change at four and seven-year cycles, representing 'SAM-like' and 'ENSO-like' climate events, respectively, and their impacts on the predicted prey availability. While we know that these cycles don't operate exactly periodically, and that in fact climate change may affect the frequency and strength of the cycle, this implementation is a necessary simplification to examine how a large-scale cycle may impact on the population.

The calculation (equation 4.1) for a change in climate variability on the effective food availability is as follows

$$\text{clim var} = \left(rv \left(\sin \left(\frac{360}{cycle} \times y \right) \right) \right) + 1 \tag{4.1}$$

where y indicates the current year in the model. The perturbation amplitudes of the climatic events are set at a range from 0.25-1.00 using rv. The sinusoidal length was determined by $cycle$; here set for four or seven years representing SAM-like and ENSO-like climate periodicity, respectively.

The effective food availability f_{eff} (equation 4.2) of individuals was modified as follows

$$f_{\text{eff}} = f_{\text{eff}} * \text{clim var} \tag{4.2}$$

and is used in addition to equation 2 of Goedegebuure et al. (2018) for f_{eff}, which implements individual variability as well as competition on the absolute food availability f_a.

Hypothesis 2 - Reduction in yearling survival

Several studies have identified a decline in first year survival as a possible driver of overall southern elephant seal population decline at Macquarie Island (see Hindell, 1991; McMahon et al., 2005a). Survival of yearlings is related to the condition of their mother; their size and mass at weaning; and their own foraging success (*e.g.* Hindell, 1991; McMahon et al., 2000; Clausius et al., 2017b). The survival rates of yearlings range from 54% for small (<95 kg) pups, to 72% for larger (>135 kg) pups (McMahon et al., 2000). Although the mean weaning mass of pups at Macquarie Island is around 117 kg (McMahon et al., 1997) male pups are on average larger than females (McMahon et al., 2000). Young seals have been shown to have different diet and foraging behaviour from those older than one year (McMahon et al., 2005a, and references therein). Non-energetic factors in pup survival include predation by

Orcas *Orcinus orca*, however, unless populations are very small this is not seen as a driver for population decline (McMahon et al., 2003).

To test if the model could match the observed decline we implement an energetics-related increase in mortality of yearlings by reducing the overall energy intake to a proportion of the population of yearlings. The reduction in energy intake starts at conception (which assumes a reduction of investment by the mother) and continues through their first year (assuming the yearling is weaker and less able to successfully fend for itself). The decision to implement this only to a selected proportion of the yearlings reflects the likelihood that not all yearlings would suffer from reduced energy intake, and that the reduction in energy would not be evenly spread across the population. We have included a reduction in energy of 20%, 50%, or 80% of the assumed intake; which is applied to 20%, 50%, or 80% of the yearlings.

Two parameters are added to the model to identify i) if an individual is affected by the reduced energy intake, and ii) by how much their energy intake reduces (SA_{change}). If the foetus is affected, two calculations in the model are modified (originally equations 26 and 28 in Goedegebuure et al., 2018); growth of the foetus dL (equation 4.3) is reduced, and the energy intake dU_E (equation 4.4) are reduced as follows

$$dL = r_B \; L_{max} \; (1 - SA_{\text{change}}/2) \tag{4.3}$$

$$dU_E = dU_E \; (1 - SA_{\text{change}}) \tag{4.4}$$

where r_B of equation 4.3 is the von Bertalanffy growth rate (equation 27 in Goedegebuure et al., 2018), and L_{max} is the maximum size reached.

For the pups (equation 4.5) and yearlings (equation 4.6) the calculations for energy intake are as follows

$$S_A = \frac{f_{\text{eff}} \; L^2}{\kappa_L} \; (1 - SA_{\text{change}}) \tag{4.5}$$

$$S_A = f_{\text{eff}} \; L^2 \; (1 - SA_{\text{change}}) \tag{4.6}$$

where S_A represents the assimilation flux for calculation of the stored energy; f_{eff} represents

the effective food availability (taking into account the absolute food availability f_a, individual variability iv and competition ΔP; see equations 1-3 in Goedegebuure et al., 2018). In both equations, L^2 is the current structural size of the individual, and for equation 4.5, κ_L is implemented to allow for the increased 'fattiness' of southern elephant seal milk (Hindell et al., 1994b; Goedegebuure et al., 2018).

Hypothesis 3 - Reduction in fecundity

As there is little to no migration between sub-populations of southern elephant seals (van den Hoff et al., 2014), a major driver to the number of new individuals recruited into the breeding population is closely related to the fecundity (or breeding success) of individuals within the population (McMahon et al., 2005a; Authier et al., 2012). To test if the model could match the observed decline in the southern elephant seal population at Macquarie Island we modified the breeding threshold of mothers.

Changes to the breeding threshold of mothers were implemented to 20%, 50% and 80% of the mothers, with increases of 20%, 50%, or 80% of the threshold. The decision to implement this only to a selected proportion of the mothers reflects the likelihood that not all mothers would suffer from reduced fecundity, and that the reduction in fecundity would not be evenly spread across the population. These implementations add two parameters to the model to i) indicate if the mother is affected by the increased energy storage requirements, and ii) by how much the breeding threshold is changed (fec_{change}). The threshold (equation 4.7) is set as follows

$$cum_{UE} = cum_{UE}\ (1 + fec_{\text{change}}) \tag{4.7}$$

where cum_{UE} is the threshold required to sustain a pregnancy (equation 10 in Goedegebuure et al., 2018). This threshold accounts for the cumulative energy requirements of pregnancy and lactation, but it has been modified in the baseline model of Goedegebuure et al. (2018) to account for a female-only population model.

Hypothesis 4 - Density dependence

The southern elephant seal population at Macquarie Island is density-regulated. As the carrying capacity (or expected equilibrium K) of the population has been reached, it incurs

high levels of competition for resources (McMahon and Burton, 2005; van den Hoff et al., 2014). To examine the potential effects of density dependence on the population structure, and to examine whether these effects will occur in an orderly fashion or display some unusual behaviour, we force a change on the population through modifying the carrying capacity (from $K_1 = 1600$ to $K_2 = 500$, at a two-yearly stepwise decline over a period of 70 years).

The rate of change r for the modelled population is calculated at the model initiation:

$$r = \frac{K_1 - K_2}{T_{\text{decline}}} \tag{4.8}$$

where T_{decline} represents the duration of the decline (here, 70 years). The rate of decline is then used to calculate the effective carrying capacity K (equation 4.9) every 2 years, starting from K_1, until $K = K_2$, following:

$$K = K - (r \times T) \tag{4.9}$$

The new carrying capacity K is then used in the calculation for competition ΔP and effective food availability f_{eff}; equations 2 and 3 in Goedegebuure et al. (2018).

Statistical analyses

For each of the hypotheses five separate Monte Carlo simulations were done. For each of the hypotheses the means of the population count over the model runs was taken and the change in the population was compared to the exponential decline observed on Macquarie Island. These observations on Macquarie Island were taken from the isthmus and include counts of female seals on the 15th of October, each year. This date is considered the day at which the maximum number of females haul out (see Hindell and Burton, 1987; McMahon et al., 2005b; Hindell et al., 2017). The observations from the isthmus are reflective of the population trends on the whole island (van den Hoff et al., 2014). To compare the model results with the observations from Macquarie Island, the time scale in the model is converted from days to years ($t = t/360$; as there are 360 days in a model year, as explained in Goedegebuure et al. (2018)). The timeframe was transformed to match observations from 1949 to 2015 (Hindell et al., 2017).

Correlation statistics are used for the comparison of population declines for each hypothesis.

For this we smooth the emergent population to a five-year running mean, and transform the modelled population counts on a log-scale for comparison of (exponential) declines. We take the observations from Macquarie Island (log-normalised) and the predicted model values at each yearly interval that matches with the dates of the observations from Macquarie Island (67 years in total, from 1949 to 2015, inclusive) to create a fitted model of observations *vs.* predictions. Using the fitted model, we calculate the Root Mean Square Error (RMSE) using *R* (R Core Team, 2017) to give the standard deviation of the model prediction error to show the model's performance. We also calculate Pearson's product-moment correlation to test for association between the observations and predictions.

For each of the hypotheses we compared results of five Monte Carlo simulations. Statistical analyses were done in R Core Team (version 3.4.1 2017) using two sided t-tests with a 99% confidence interval. The t-test is calculated using a sample size of five, where each sample size is calculated as the mean of five years at the end of the simulation (representing observations between 2010 and 2015).

4.3 Results

Life tables

A life table was generated for the female southern elephant seals on Macquarie Island, using input data derived from longitudinal capture-mark-recapture (CMR) studies at Macquarie Island, using the CMR program MARK (White and Burnham, 1999) to estimate survival and capture probabilities after weaning, as per McMahon et al. (2003). An assumption has been made in the development of the life table for the Macquarie Island southern elephant seal population (Table 4.1) that the rate of survival of females from age 7 is continuous (see McMahon et al., 2005b, and references therein), while that of the DEB-IBM presents emergent data for all age groups.

Life tables were derived from the DEB-IBM for each scenario. To do so, all new individuals (pups) born at year 90 of the model are tracked each day of their lives. We selected this year as if allows for the modelled population to have adjusted to the implemented scenario, and for the tracked individuals to reach the maximum life span during the model run. While these marked individuals are 'alive' they are counted daily, and at each year the mean number of pups they have produced is recorded. This information is used in the statistical analysis

program *R* (R Core Team, 2017) using the package *fishmethods* (Nelson, 2017) which calculates mortality and survival rates as per Krebs et al. (1989).

The life table for female southern elephant seals from Macquarie Island (Table 4.1) shows an exponential decline in the overall rate of survival l_x per age group, between birth and 15 years of age, where only 3.2% of individuals survived to 15 years old, to a maximum age of 23 (Hindell and Burton, 1988b). There is a steeper decline in the survival of yearlings (age group 1) than in later years.

Table 4.1. Life table developed from capture-mark-recapture (CMR) studies on female southern elephant seals from Macquarie Island, where p_x = Finite rate of survival during the age interval X to X+1; l_x = Proportion of individuals surviving at the start of age interval X; d_x = Proportion of individuals of a cohort dying during the age interval X; q_x = Finite rate of mortality during the age interval X to X+1.

	surv rate	surv prop	mort prop	mort rate
Age group	p_x	l_x	d_x	q_x
Birth		1		
0-1	0.696	0.696	0.304	0.304
1-2	0.816	0.568	0.128	0.184
2-3	0.834	0.463	0.104	0.184
3-4	0.866	0.387	0.077	0.166
4-5	0.797	0.335	0.052	0.134
5-6	0.779	0.267	0.068	0.203
6-7	0.800	0.208	0.059	0.221
7-8	0.832	0.166	0.042	0.200
8-9	0.826	0.138	0.028	0.168
9-10	0.759	0.114	0.024	0.174
10-11	0.742	0.087	0.028	0.241
11-12	0.751	0.064	0.022	0.258
12-13	0.758	0.048	0.016	0.249
13-14	0.868	0.037	0.012	0.242
14-15	0.733	0.032	0.005	0.132

The cumulative survival of individuals in the baseline model of Goedegebuure et al. (2018) is somewhat different from the cumulative survival of females on Macquarie Island (Figure 4.1;

Tables 4.1 & A4). While the survival of yearlings in the baseline model (67.3%) is close to that of yearlings on Macquarie Island (69.6%), the observations on Macquarie Island indicate an exponential decay in cumulative survival. This is only visible in the baseline model results from age ten onwards. The Gaussian decay that is shown by the model may be due to the survival rates in the model being too high for individuals between age two and four. This is likely because we do not understand (and so are limited in our ability to model) processes such as predation, disease, metabolism and physiology and the costs associated with the onset of breeding. These are all important processes to try to focus future research effort on. For the purposes of our model, we assumed that the rate of survival is reasonable after the first year, as the first year is the most difficult for the seals to get through, having been left alone following weaning, and needing to find food on their own. This is further discussed in Chapter 5.

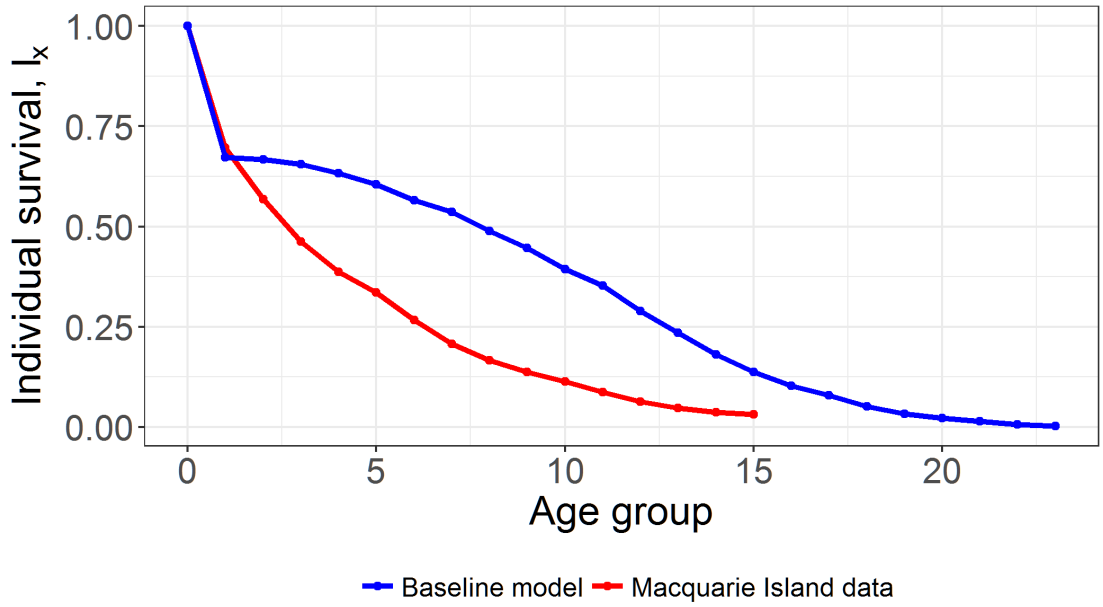

Figure 4.1. A comparison of the proportion of individuals surviving from one age group to the next l_x, in the baseline model (blue) and Macquarie Island observations (red).

Each of the four hypotheses that are tested using this DEB-IBM are drawn from studies of the population status and trends of southern elephant seals and their breeding and foraging behaviour at Macquarie Island. The scenarios are, by necessity, simplified interpretations of intrinsic or extrinsic factors. Nonetheless the following results and discussion show how a DEB-IBM such as this one can be used for interpretations of real-world events.

Hypothesis 1 - Climate variability

To test if hypotheses surrounding climate variability near the foraging grounds of southern elephant seals on Macquarie Island could be the driver behind the observed exponential population decline we implemented two separate scenarios to our DEB-IBM. We have simulated climate variations representing the Southern Annular Mode (a four-year cycle representing SAM-like simulation) and El Niño Southern Oscillation (a seven-year cycle representing ENSO-like simulation) by implementing sinusoidal changes in the effective food availability on four and seven-year cycles, respectively. This implemented interannual variation in the model gives a relative food availability of 100% in 'good' years but causes a serious reduction in food availability in 'bad' years (especially for higher perturbation amplitudes).

Considering the long recovery time of long-lived populations (Eberhardt, 2002), we expect that the population responds quickly to reductions in food availability, and slower to increases, and therefore that 'bad' years have a more immediate effect on the population than good 'years'. The population may not stabilise with annual changes; however we expect some stability to happen where there are longer periods between the good and bad years. As the model is not spatially explicit the simulations surrounding climate variability are only an interpretation of real-world events. The environmental variability in the model lacks stochasticity and thus cannot accurately represent environmental variation as actual climatic events are much more irregular which could include larger or smaller amplitudes between years.

The Southern Annular Mode

Implementing a four year sinusoidal variation of the effective food availability, representing a SAM-like climate event, at amplitudes ranging from 0.2 to 1.00 (which at a perturbation amplitude of 1.00 ultimately leads to periods with zero food availability) caused an artificial perturbation to the population (Figure 4.2A) immediately after implementation of the scenario. The populations experienced a steep decline due to sudden deaths of individuals who were affected by the sudden implemented change in the resource availability. The population in simulations with low amplitudes recovered after $\sim$10-20 years, close to the original population size, at year $\sim$1950. This is likely the point at which the artefact is no longer artificial. At amplitudes higher than 0.80 there were sustained declines in the populations following the implementation of the scenario (from year $\sim$1950 onwards). For further analyses of the hypothesis the modelled population at an amplitude of 0.985 is used (Figure 4.2A).

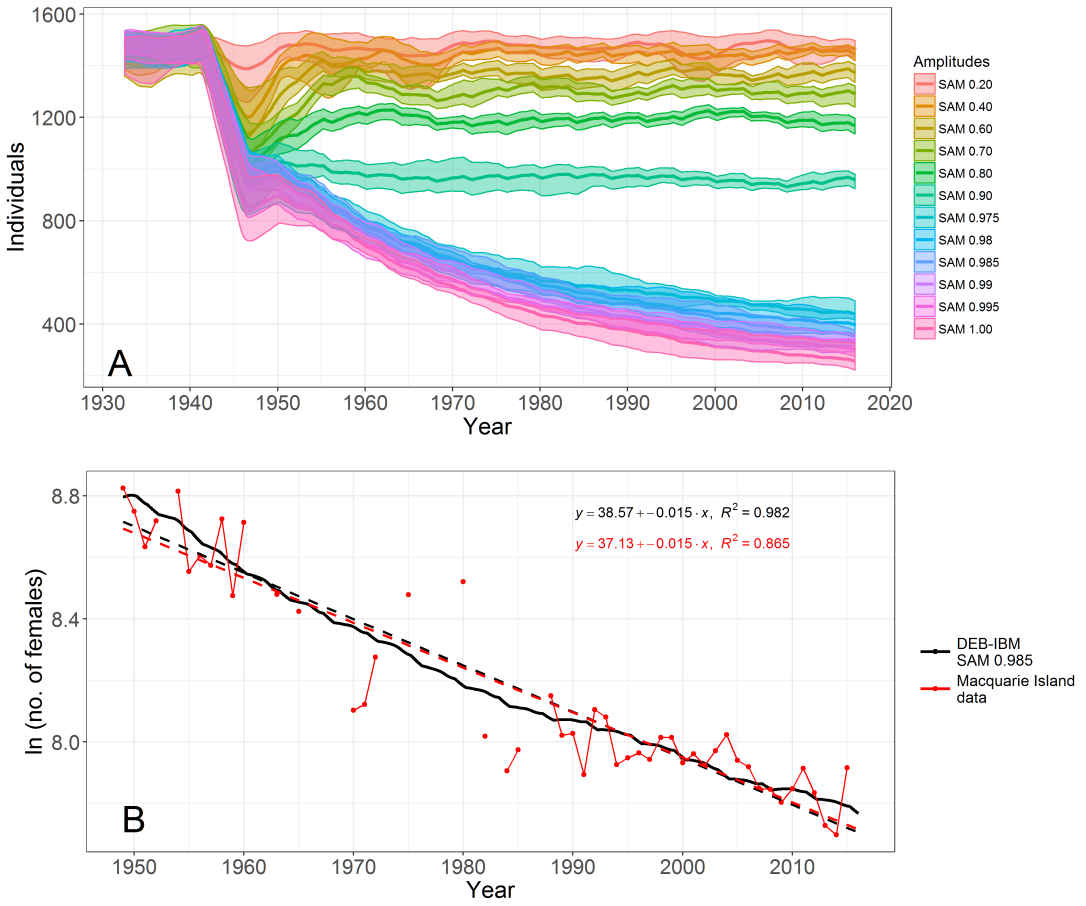

Figure 4.2. Comparison of population trajectories with implemented change on the model reflecting a sinusoidal change in the effective food availability of individuals, on a four-year cycle to represent Southern Annular Mode (SAM-like) climate events. A) Amplitudes of the events are increasing from 0.2 to 1.00, following equations 4.1 and 4.2 in text; implemented at year 1940 in the model. The populations at all amplitudes experience a perturbation to the system at the implementation of the model after which the populations recover over time, and at low amplitudes return to a stable population. The modelled population results have been scaled to fit on the same time scale as the observations at Macquarie Island, through addition of 1930 years to the timeline. The modelled population at an amplitude of 0.985 is used for further analyses of the hypothesis. B) Log-normalised modelled population at an amplitude of 0.985, overlayed on log-normalised counts of female southern elephant seals from the Isthmus on Macquarie Island (red; 1949-2015). The modelled population results have been scaled to fit on the same log-scale as the observations, through multiplication of the modelled individuals ($\times$ 6.7). The exponential rate of change of the model (black, dashed) is at -1.53% ($F = 2628_{(1,47)}$; p <0.01; $R^2 = 0.98$), compared to the observations (red, dashed) at -1.46% ($F = 301.3_{(1,47)}$; p <0.01; $R^2 = 0.86$ (see Hindell et al., 2017)). Pearson's product-moment correlation of model results compared to the observations (red) was 0.94, with a Root Mean Squared Error (RMSE) of 0.112.

The rate of decline of the modelled population was similar to that observed at Macquarie Island with a perturbation amplitude of the scenario of 0.985 (with the first 17 years of the results removed from the analyses to let the population adapt to implemented changes in the effective food availability; Figure 4.2B), where the population decline was -1.53% per year between 1949 and 2015 ($R^2 = 0.98$) compared to -1.46% per year ($R^2 = 0.86$) observed in the southern elephant seal population at Macquarie Island over the same timeframe. Analyses of the population decline in the model at similar amplitudes showed that a change of 0.005 either way resulted in a population decline of -1.41% and -1.64% per year, respectively for amplitudes of 0.98 and 0.99.

For the chosen simulation there were significant changes in the population dynamics compared to the baseline model of Goedegebuure et al. (2018). The proportion of the population that comprises of juveniles and adults was, at the start of the simulation, similar to the baseline model, but as soon as the scenario was implemented adults in the population died, causing a spike in the percentage of the population that was made up of juveniles. The proportion of the population comprised of juveniles and adults swapped over the duration of the simulation. These juveniles then continued reproducing, and over $\sim$20 years brought the population dynamics back to a stable equilibrium (see Figure 4.3, and Table 4.2, column 1, and Table A3).

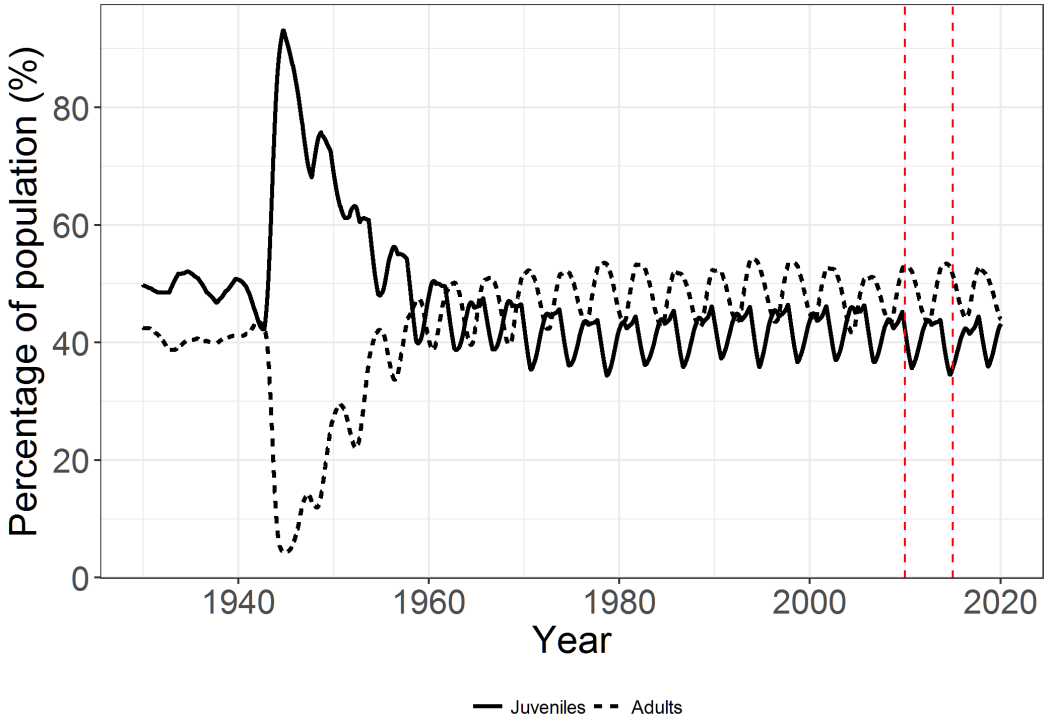

Figure 4.3. A comparison of the percentage of the modelled population that consists of juveniles (black, solid) and adults (black, dashed) over the duration of the simulation representing Southern Annular Mode (SAM-like) climate events. The red dashed lines indicate the period of the simulation used for data analyses of Table 4.2, column 1, from 2010-2015. The modelled population results have been scaled to fit on the same time-scale as the observations, through addition of 1930 years to the timeline. The initiation of the SAM simulation in the model was at year 1940 (see also Figure 4.2A) after which there was a clear shock to the population, for which it took ∼20 years to recover.

Table 4.2. Population dynamics and emergent behavioural changes of the model at the end of the simulation with scenarios for Hypotheses 1 (Southern Annular Model (SAM-like), and El Niño Southern Oscillation (ENSO-like) climate variations), Hypothesis 2 (reduction in yearling survival), and Hypothesis 4 (density dependence scenario). Results for Hypothesis 3 (reduction in female fecundity) are presented in Table 4.3. Results presented in the table are the means (± standard deviation) of the last five years (representing years 2010-2015) of the simulations, where grey boxes indicate a significant difference (p <0.01) between results from the stable population in the baseline model of Goedegebuure et al. (2018, Table A3) and the scenario simulation. Results for lifespan of individuals exclude deaths of yearlings; proportion of juveniles excludes count of yearlings.

	Hypothesis 1		Hypothesis 2	Hypothesis 4
	SAM	ENSO	Yearling Survival	Density Dependence
Population size *	369±38	251±18	538±58	950±49
Percentage of juveniles in population **	42.04±1.22%	47.37±0.84%	32.23±0.36%	56.61±2.61%
Percentage of adults in population **	49.71±1.44%	43.34±0.91%	48.94±0.48%	34.84±2.39%
Pup survival	97.60±0.25%	95.66±2.17%	98.15±0.60%	97.37±0.65%
Yearling survival	63.81±0.25%	60.47±17.54%	33.64±1.70%	57.88±2.23%
Age at first reproduction (yr)	4.40±0.00	4.40±0.00	4.40±0.00	4.40±0.00
Generation time (yr)	7.84±0.27	8.33±0.32	9.92±0.27	8.05±0.45
Juvenile age (yr) ***	3.05±0.05	2.70±0.05	3.58±0.11	4.82±0.37
Min adult (transition) age (yr) ***	5.65±0.13	5.67±0.18	4.66±0.11	5.25±0.12
Adult age (yr) ***	10.29±0.17	9.71±0.14	11.53±0.22	10.79±0.46
Lifespan (yr)	11.05±0.35	10.20±0.36	12.79±0.48	12.03±0.27
Max lifespan (yr)	23.70±2.19	23.54±2.99	27.95±1.53	24.99±0.128
Fecundity	0.26±0.01	0.33±0.01	0.42±0.01	0.25±0.01
Max number of births per mum	4.80±1.79	6.00±1.22	9.80±1.10	6.00±0.94
Juvenile size (cm)	166±0.28	162±0.44	161±0.87	171±0.85
Adult size (cm)	193±0.21	195±0.17	208±0.74	187±0.65
Max size (cm)	205±1.40	208±1.59	236±0.49	190±0.71
Relative food availability for (age >360 d)	0.79±0.00	0.67±0.00	0.97±0.00	0.72±0.05

The mean ages of juveniles, adults and the mean age at transition from juvenile to adult changed significantly between the baseline model of Goedegebuure et al. (2018) and the SAM-like scenario (Table 4.2, column 1). The age at transition from juvenile to adult remained relatively similar over the whole model period, although the age increased between beginning and end of the simulation, whereas both the mean ages of juveniles and adults experienced a large change at the time where the scenario was implemented in the model. The overall drop in the mean juvenile age (compared to the baseline model; see Table 4.2, column 1, and Table A3) may indicate that fit juveniles have an increased ability to forage and accumulate energy stores, allowing them to transition to adult stage sooner.

Justification of this change in the mean age of juveniles can also be backed by the comparison of sizes of juveniles and adults, who are all larger at the end of the simulation, than in the baseline model (168$\pm$0.16 cm compared to 193$\pm$0.21 cm for juveniles, and 193$\pm$0.59 cm compared to 205$\pm$1.40 cm for adults; Table 4.2, column 1, and Table A3). Additionally, the survival of yearlings is higher in the model for the SAM-like climate event than the baseline model.

During simulations for a SAM-like climate scenario, the majority of female southern elephant seals started breeding at four years of age (Figure A1), with the remainder breeding at five years of age (Table A5). At the ages of six to eight, the mothers struggle with their second birth, and the majority put off getting pregnant until later. In the baseline model mothers predominantly wait until five or six years old for their first birth, but maintain a more stable fecundity after that (Table A5, Figure A1). The fecundity during the SAM-like climate simulation followed the oscillating behaviour of the changes in effective food availability (Figure 4.4); fecundity dropped to zero following years where there was little to no resources available, and increased in years following normal to high resource availability.

El Niño Southern Oscillation

The sinusoidal changes, over a seven-year cycle, in the effective food availability representing El Niño Southern Oscillation (ENSO) 'like' events result in a more variable population than the four yearly cyclic changes representing SAM-like events. The increase in the period over which the changes are implemented (*i.e.* there are longer periods with reduced to no food available to individuals) means that the population must recover from more severe negative effects. Variations with identical amplitude of the SAM-like climatic variations have much stronger negative effects on the population when implemented on ENSO-like cycles. For

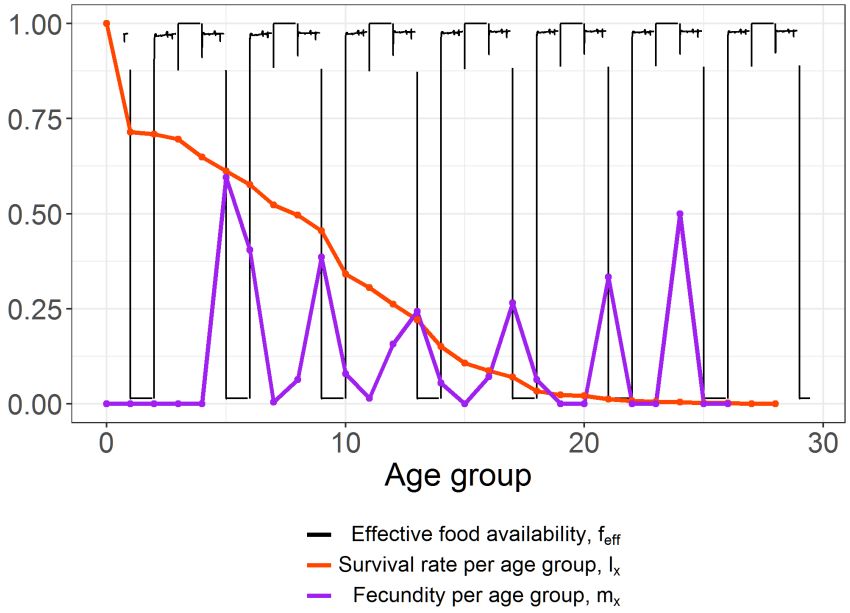

Figure 4.4. Comparison of the mean level of effective food availability of individuals f_{eff} (black); the proportion of individuals surviving at the start of age interval X l_x (orange) and the mean fecundity of a cohort during the age interval X f_x (purple) over the age groups (a 30 year time frame) of the model simulation for representation of population dynamics during a SAM-like climatic event. The survival rate and fecundity are as per Table A5; the mean effective food availability is presented in Table 4.2, column 1.

example perturbation amplitudes >0.80 cause a population collapse within the duration of the model simulations (Figure 4.5A).

Although the population regains stability after an initial steep decline in numbers at lower amplitudes (<0.40), there is a high degree of variability. At amplitudes of the cyclic ENSO-like events between 0.20 and 0.60 the population seems to recover to baseline levels, however periods with sufficient resource availability are too short and the population almost immediately experiences a steep decline again. The initial steep decline observed in the model population at year 1940 is a shock response by the population upon initialisation of the scenario to the model. At higher amplitudes (>0.70) the population continues to decline, with population collapse occurring when resource availability is too low for extensive periods (Figure 4.5A). For further analyses of the hypothesis on climate variations, representing ENSO, a perturbation amplitude of 0.744 is used.

Comparisons of the log normalised model population and observed population at Macquarie Island show that the exponential rate of change of the model (-1.56%, $R^2 = 0.98$; Figure

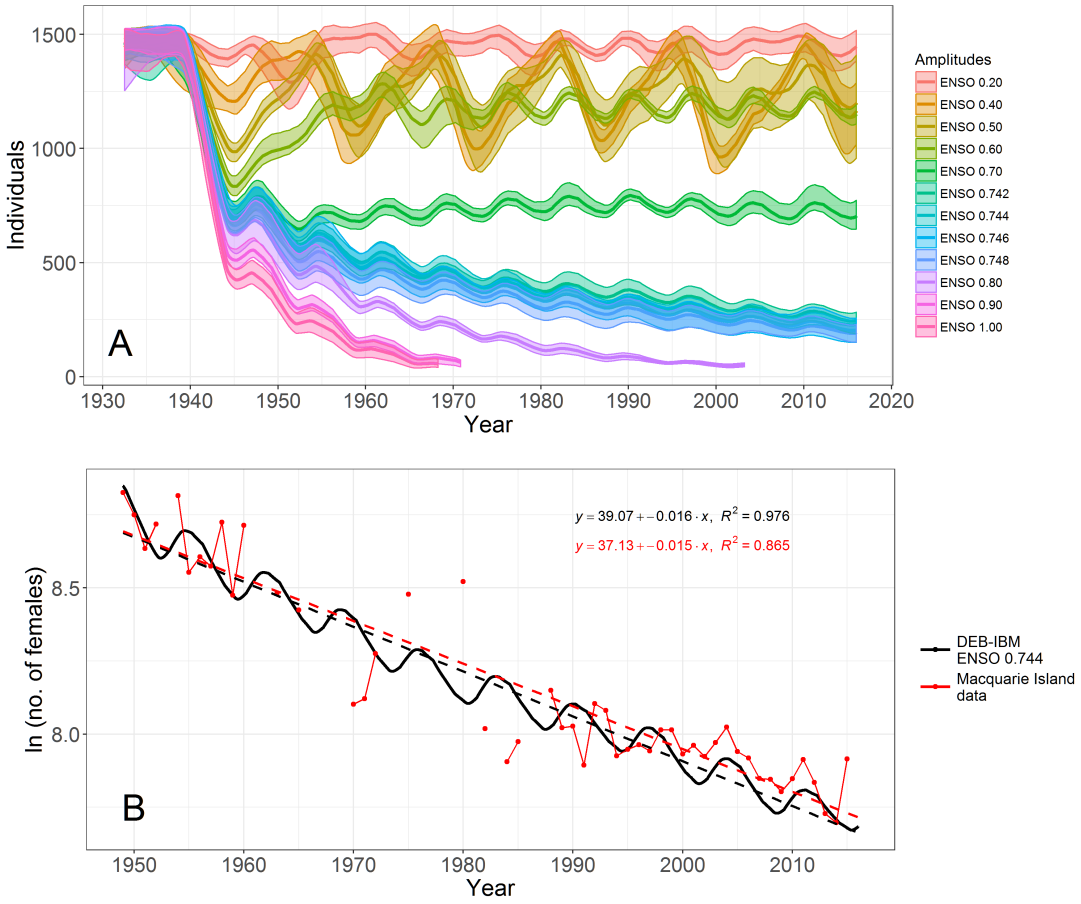

Figure 4.5. Comparison of population trajectories with implemented change on the model reflecting a sinusoidal change in the effective food availability of individuals, on a seven-year cycle to represent El Niño Southern Oscillation (ENSO-like) climate events. A) Perturbation amplitudes of the ENSO-like events are increasing from 0.2 to 1.00, following equations 4.1 and 4.2 in text, and implemented at year 1940 in the model. The populations at all amplitudes experience a 'shock to the system' at the implementation of the model after which the populations recover over time at a low amplitude (0.20); at higher amplitudes, the model is unable to maintain stable populations. The modelled population results have been scaled to fit on the same time scale as the observations at Macquarie Island, through addition of 1930 years to the timeline. The modelled population at a perturbation amplitude of ENSO 0.744 is used for further analyses. B) Log-normalised modelled population at an amplitude of 0.744 overlayed on log-normalised counts from the Isthmus on Macquarie Island (red; 1949-2015). The modelled population results have been scaled to fit on the same log-scale as the observations, through multiplication of the modelled individuals ($\times$ 9.5). The exponential rate of change of the model (black, dashed) is at -1.56% ($F = 1938_{(1,47)}$; p <0.01; $R^2 = 0.98$), compared to the observations (red, dashed) at -1.46% ($F = 301.3_{(1,47)}$; p <0.01; $R^2 = 0.86$ (see Hindell et al., 2017)). Pearson's product-moment correlation of model compared to the observations (red) was 0.92, with a Root Mean Squared Error (RMSE) of 0.131.

4.5B) is similar to the -1.466% decline in the Macquarie Island population per year ($R^2 = 0.86$) between 1949 and 2015. Although the Pearson's product-moment correlation of the model compared to the population observations of Macquarie Island were high (0.92), the RMSE at 0.131 indicates that although the model can follow the overall decline observed in the southern elephant seal population at Macquarie Island, it does not represent the significant variability in the population that is overlaid against the long-term decline, as was observed between 1949 and 1990.

Behavioural and life history results of the population after implementation of the ENSO-like events, at a perturbation amplitude of 0.744, show that the modelled population is structurally affected by the changes (Table 4.2, column 2). There are only four emergent features which were not significantly different from the baseline model of Goedegebuure et al. (2018); yearling survival, age at first breeding, generation time and maximum lifespan. The percentage of the population made consisting of juveniles and adults shows a significant difference from the baseline model; after the initial shock to the population following the implementation of the scenario to the model (at year 1940, Figure 4.6), the population dynamics changed from having a population with approximately 50% juveniles to a population where the percentage of juveniles and adults within the population oscillate over a seven-year cycle. The oscillations reduce in intensity over time with smaller percentages of juveniles in the population near the end of the model simulation, indicating that the population is slowly becoming accustomed to the implemented changes, and could potentially stabilise again if run over longer time frames.

The mean ages of juveniles, adults, and the mean age at transition from juvenile to adult were significantly different from the baseline model (Table 4.2, column 2). These mean ages oscillate heavily after implementation of the scenario. Where the mean juvenile age ranged from $<$2 years old, to $>$4 years old; similarly, for the mean adult ages, ranging from $<$9 years, to $\sim$11 years old. And although the transition age had the smallest observed oscillation, the range between 5 and 6.5 years old was still much higher than the mean baseline age. The mean lifespan of individuals in the ENSO-like simulation was significantly lower than that of the baseline model, at 10.20$\pm$0.36 and 10.74$\pm$0.06, respectively (Table 4.2, column 2, and Table A3).

There is no significant difference observed between the survival rates of yearlings over the ENSO-like simulation (60.47$\pm$17.54%; Table 4.2, column 2) and the baseline model (65.76$\pm$2.17%; Table A3), although there is a major increase in the variation between years. The life table (Table A6) for the ENSO-like simulation shows the extreme mortality observed

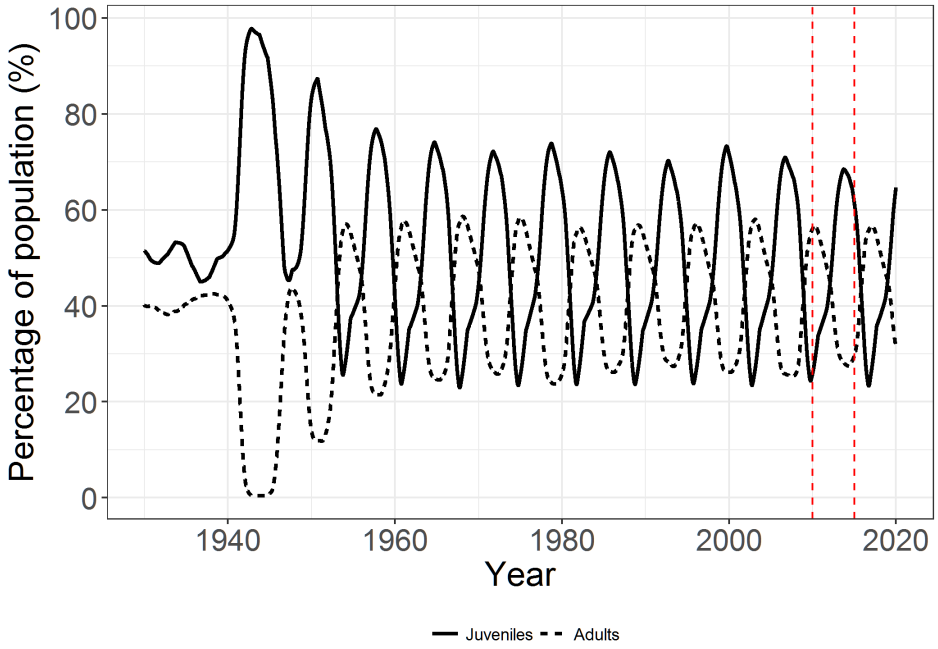

Figure 4.6. A comparison of the percentage of the modelled population that consists of juveniles (black, solid) and adults (black, dashed) over the duration of the simulation representing the El Niño Southern Oscillation (ENSO-like) simulation. The red dashed lines indicate the period of the simulation used for data analyses of Table 4.2, column 2. The initiation of the ENSO-like simulation in the model was at year 1940 (see also Figure 4.5A) after which there was a clear shock to the population.

in the first year of the modelled individuals, with survival rates as low as 28.7% (Figure A2A). This range in the yearling survival is seen throughout the model simulation (Figure 4.7) with survival as low as 10% and up to 85% some years later. This variation in the emergent yearling survival rate may be due to the different years the pups are born. If they are born in years with low resources, the yearlings may struggle to gain enough energy for survival. Similarly, when there is excess food available at the opposite end of the cycle, yearling survival increases as yearlings are able to gain enough energy. Alternatively, if pups are born following periods of low resource availability, mothers may not have enough energy to pass on to their offspring and yearlings have a lower chance of survival.

The mean fecundity (0.33$\pm$0.01; Table 4.2, column 2) during the ENSO-like scenario was significantly higher than that of the baseline model (0.28$\pm$0.00; Table A3) with all individuals that have survived to reproductive age, giving birth between four and five years of age (m_x, Table A6), compared to $<$25% of four to five year olds of the baseline model (Figure A2B).

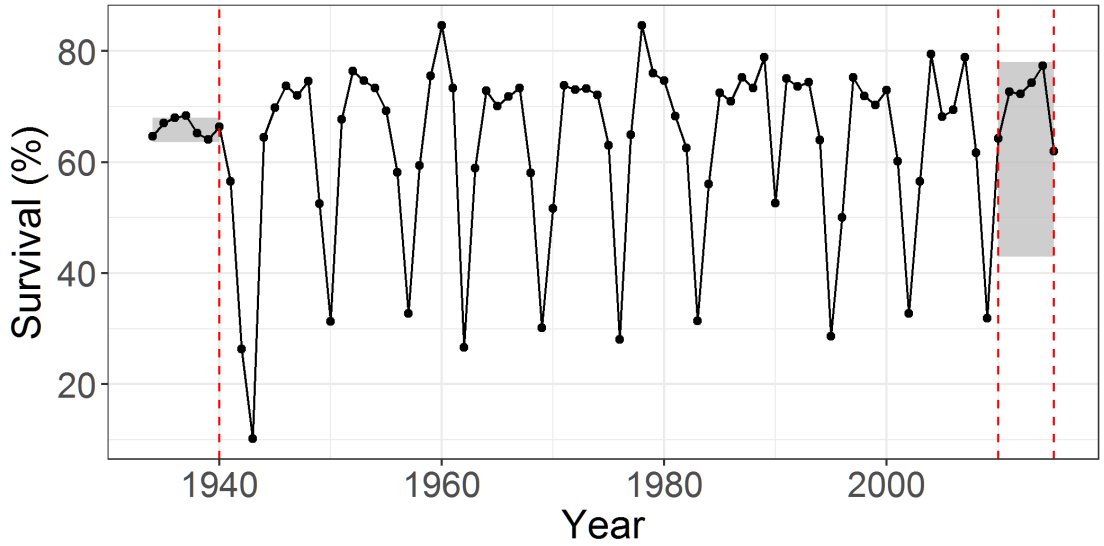

Figure 4.7. A comparison of the yearling survival during the model period for El Niño Southern Oscillation (ENSO-like) simulation at a perturbation amplitude of 0.744. The initiation of the model was at year 1940 (red dashed line, see also Figure 4.5A) after which the yearling survival experienced significant oscillation. The grey boxes show the baseline results of Goedegebuure et al. (2018), pre-1940, and the results of the simulation (red dashed lines representing 2010-2015; Table 4.2, column 2).

Even with the increased fecundity, however, the total number of births (6.00±1.22; Table 4.2, column 2) by mothers over their lifespan was still lower than that of the baseline model (8.9±1.10; Table A3), ultimately leading to a reduction in the modelled population.

Hypothesis 2 - Reduction in yearling survival

To test if the hypothesis surrounding a reduction in yearling survival could be the driver of the observed exponential decline of southern elephant seals at Macquarie Island we implemented a scenario that reduces the expected energy intake of yearlings from conception to one year of age. As individual variability is accounted for in the model, and southern elephant seals have an energy buffer (fat storage) for 'bad' times, we expect that a small change in the energy consumption by pups would not have a great impact on the stability of the population. At a larger change, however, we expect that there will be increased pup mortality in the model that may affect the population stability over time.

Analyses of the model were done on population projections, to see which, if any, of the model runs would be able to be used in comparison to observed declines in the southern

elephant seal population on Macquarie Island. Each of the model runs for this hypothesis showed a delay of ∼10 years after which the effects of the changes were observable in the population projections. This is because this hypothesis, unlike hypothesis 1 (which was a 'globally' implemented change), is based on individual changes, which take time to develop into a population response. The population projections of the model with 20% of the yearlings affected (Figure 4.8A) showed a small reduction to the overall population, however remained stable at each simulation of the energy reductions (20, 50, or 80%). This was expected to happen as the population adapted to the implemented changes with the emergent mortality rates being similar to those already included in the model. The expected first year survival rate of southern elephant seals ranges from 54% to 72% (McMahon et al., 2000). For the simulation with 20% of the yearlings affected by reduced energy intake, the mean mortality rate is thus captured in the simulation (*i.e.* those individuals who were expected not to survive already, were more adversely impacted by the implementation of the scenario and died).

Reductions of energy affecting 50% of the yearlings caused significant population declines for each implemented change (Figure 4.8B), with reductions of 80% of the energy intake causing the population to collapse near the end of the simulated time frame. The population could not recover from having 80% of the yearlings affected by any reduction of their energy intake (Figure 4.8C); each of the 15 simulations at 80% of the yearlings affected resulted in a collapse of the population. Following the initial results of overall population behaviour at varying levels of reduced energy intake, further analyses and comparisons with the observed population at Macquarie Island and with the baseline model use only the modelled population affected by a 50% reduction of energy, to 50% of the yearlings (Figure 4.8B, green).

The log-normalised population of simulations with a 50% energy reduction, applied to 50% of the yearlings (Figure 4.8B, green) showed the most similar rate of change as the observed population at Macquarie Island (-1.49%, $R^2 = 0.93$, compared to -1.46%, $R^2 = 0.87$ for Macquarie Island; Figure 4.8D). The Pearson's product-moment correlation of the model's rate of change and the island observations ($corr = 0.93$) and the RMSE of 0.012 indicates that the model result is highly correlated with the island observations. The outliers in the observations, however, are not well represented by the model as the modelled population follows a decline without large variations, and there is a steeper decline in the modelled population prior to 1980 compared to the period after 1980.

The percentage of the population made up by juveniles and adults was stable in the baseline model of Goedegebuure et al. (2018) which after implementation of the scenario changed significantly (Table 4.2, column 3, Figure 4.9). These new dynamics in the population took some

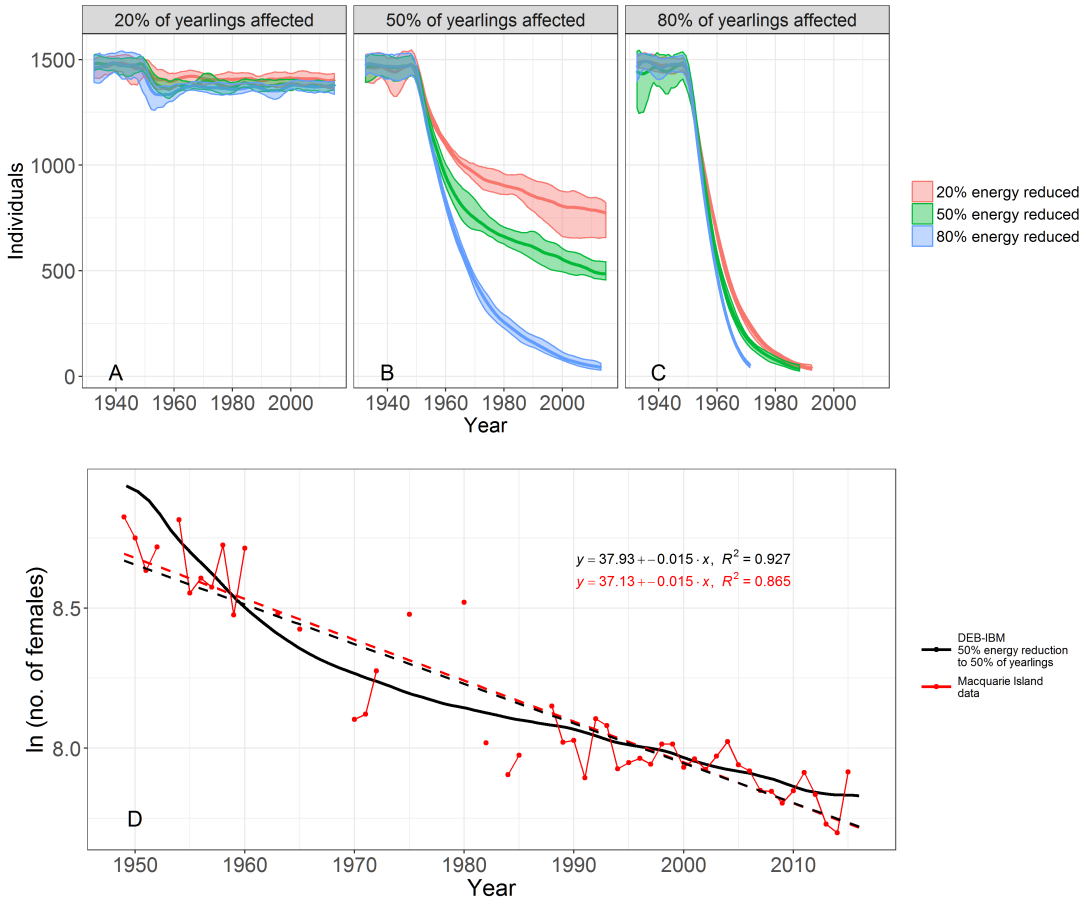

Figure 4.8. Comparison of modelled population trajectories with implemented change in the model reflecting a reduction in the intake of energy. Comparisons for 20% (A), 50% (B), or 80% (C) of the yearlings affected by a 20% (red), 50% (green), or 80% (blue) reduction in energy intake, following equations 4.3, 4.4, and 4.5; implemented at year 1940, 20 years after run-in period. The modelled population results have been scaled to fit on the same time scale as the observations at Macquarie Island, through addition of 1930 years to the timeline. The modelled population at a 50% reduction of energy, to 50% of the yearlings (facet b, green) is used for further analyses. D) Log-normalised modelled population overlayed on log-normalised counts from the Isthmus on Macquarie Island (red; 1949-2015). The modelled population results have been scaled to fit on the same log-scale as the observations, through multiplication of the modelled individuals ($\times$ 5.2). The exponential rate of change of the model (black, dashed) is at -1.49% ($F = 599_{(1,47)}$; p <0.01; $R^2 = 0.93$), compared to the observations (red, dashed) at -1.46% ($F = 301.3_{(1,47)}$; p <0.01; $R^2 = 0.86$ (see Hindell et al., 2017)). Pearson's product-moment correlation of model compared to the observations was 0.93, with a Root Mean Squared Error (RMSE) of 0.012.

time to emerge and be maintained. The reduced survival of yearlings (from 65.76±2.17% in the baseline model of Goedegebuure et al., 2018, Table A3, to 33.64±1.70%, Table 4.2, column 3, Figure 4.10; and see also Table A7) has a significant effect on the overall population dynamics and behaviour, and ultimately driving the change in the adult to juvenile proportion (as seen in Figure 4.9). The mean age at transition from juvenile to adult stage (Table 4.2, column 3) as well as the mean ages of juveniles and adults were significantly different from the baseline model. Although the mean juvenile and transition ages were lower than those of the baseline model, the mean adult age was almost a year higher. This is due to fewer juveniles surviving, thus driving up the mean age of adults.

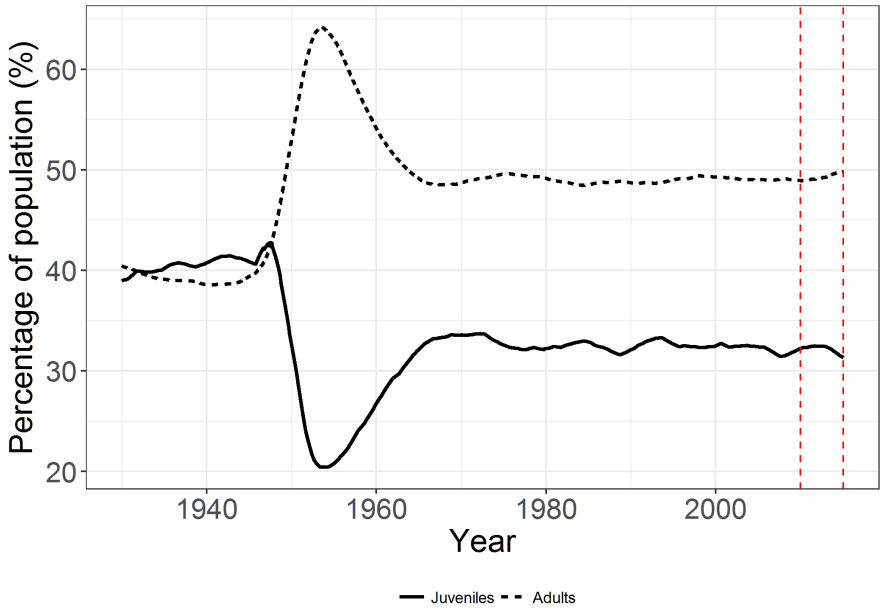

Figure 4.9. A comparison of the percentage of modelled population that consists of juveniles (black, solid) and adults (black, dashed) over the duration of the simulation where 50% of the yearlings are affected by a 50% reduction in energy intake. The red dashed lines indicate the period of the simulation used for data analyses (Table 4.2, column 3). The initiation of the simulation was at year 1940 (see also Figure 4.8A-C) after which there was a delayed response by the population to the change in events.

The mean fecundity is significantly higher in the hypothesis simulation than the baseline model (0.42±0.01 compared to 0.28±0.00), having almost doubled. Mothers give birth to one more pup in their lifetime (Table 4.2, column 3) as they expended significantly less energy to 50% of their pups from at conception (see section 4.2). The reduced energy they allocated to pups, improves their own overall fitness; allowing the mothers to produce more pups. The age at first reproduction (nor the generation time), however, were not significantly different

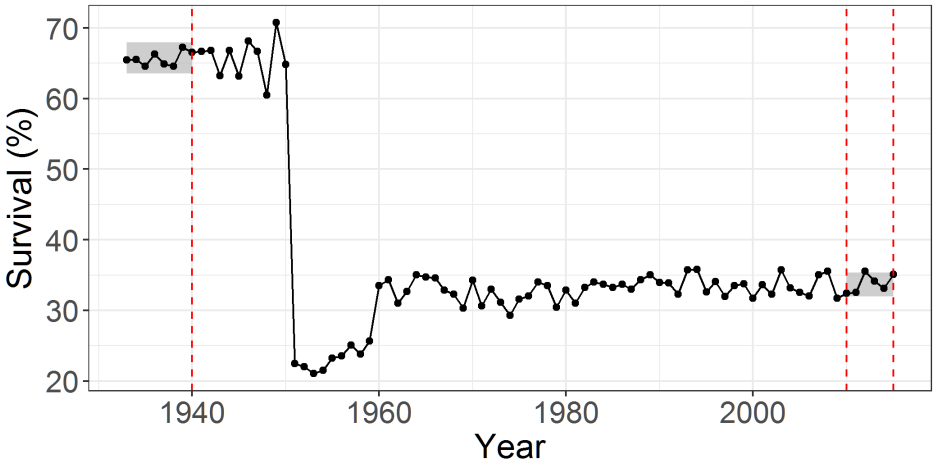

Figure 4.10. A comparison of the survival by yearlings from the baseline model, over the duration of the simulation where 50% of the yearlings are affected by a 50% reduction in energy intake. The initiation of the simulation was at year 1940 (see also Figure 4.8A-C) after which there was a delayed response by the population to the change in events. The grey boxes show the baseline results of (Goedegebuure et al., 2018) (pre- 1940) and at the end of the simulation (representing 2010-2015; Table 4.2, column 3) as indicated by the red dashed lines.

from the baseline model (Table 4.2, column 3). First time mothers in the baseline model needed to recover from having given birth at the age of four or five, mothers in this scenario show less of a requirement to recover (Figure A3), as the mean fecundity fluctuates less over the age classes; births here occur closer to every other year, compared to the baseline model, where births occur fewer than one in every three years (see also Table A7).

A consequence of the reduced energy intake of 50% of the pups/yearlings is that the mean juvenile size is significantly smaller than that of the baseline model (161$\pm$0.87 cm and 168$\pm$0.16 cm, respectively), and with the reduced survival of yearlings, the overall mean size of adults, as well as the mean maximum size reached, is significantly higher than the baseline (Table 4.2, column 3, and Table A3). With the maximum size at 236$\pm$0.49 cm being closer to the expected mean size of adult southern elephant seals of Macquarie Island, than even the baseline model (Goedegebuure et al., 2018).

Hypothesis 3 - Reduction in fecundity of mothers

To test if the hypothesis surrounding a reduction in fecundity could be the driver of the observed exponential decline of southern elephant seals at Macquarie Island we implemented

a scenario that increases the reproductive threshold of mothers (using a 20%, 50% or 80% change in the breeding threshold of 20%, 50% or 80% of the potential mothers). We expected that a small increase in the breeding threshold would affect the individual's fecundity and will over time cause a change in the population. A larger change to the breeding threshold may cause a collapse in the population—either because too few pups are born due to the high threshold, or because too many mothers die due to a threshold that is too low, as they can then not sustain themselves enough to survive (incrementally causing fewer pups to be born in consecutive years). The model showed, no exponential decline for any of the scenario simulations and the simulations with larger implemented changes showed a more negative response in population responded over time compared to those with lower implemented changes (Figure 4.11a-c).

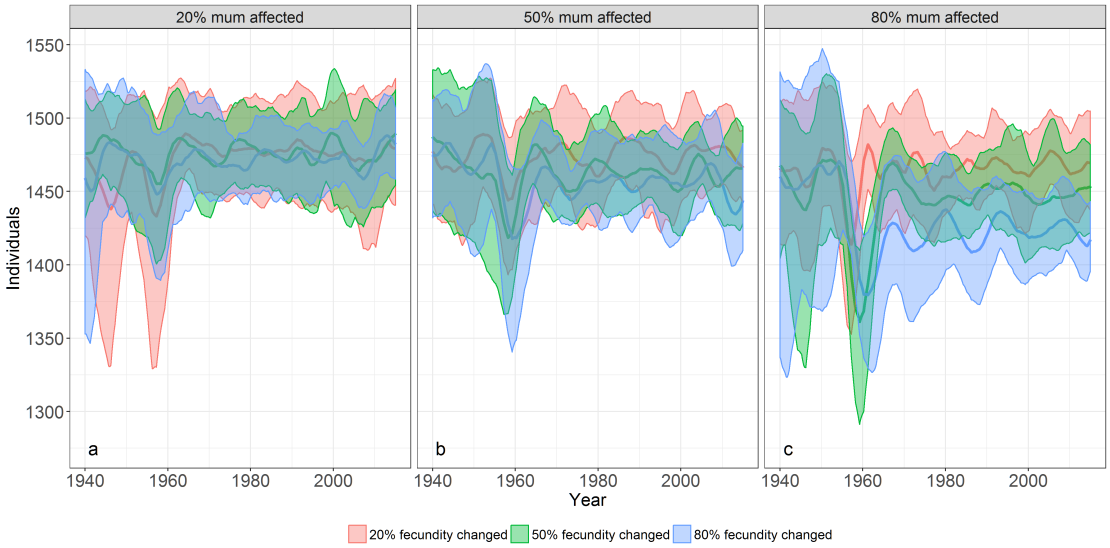

Figure 4.11. Comparison of modelled population trajectories with implemented change on the model reflecting an increase in the breeding threshold of 20% (red), 50% (green), or 80% (blue) for 20% (facet a), 50% (facet b), or 80% (facet c) of the potential mothers in the population. The modelled population results have been scaled to fit on the same time scale as the observations at Macquarie Island, through addition of 1930 years to the timeline. The modelled population at a 50% reduction of energy, to 50% of the yearlings (b, green) is used for further analyses of the hypothesis on changes in yearling survival being the potential driver behind the observed decline of the southern elephant seal population at Macquarie Island.

As for hypothesis 2, each of the model runs for this hypothesis showed a delay of ∼10 years after which the effects of the changes were observable in the population projections. This is because as this hypothesis, too, is based on individual changes. The simulations with the

implementation of changes to the breeding threshold show little change in the population trajectory over the duration of the model run at 20% of the potential mothers affected by any implemented change in the threshold (Figure 4.11a). There is a small decrease in the population size following the implementation of the scenario, however, the population quickly recovers and remains stable for the duration of the model run. At 50% of the potential mothers affected by an increase in the breeding threshold (Figure 4.11b) there is still little change in the population trajectory over the duration of the model. As with the simulation where 20% of the mothers are affected by a change in the breeding threshold there is a drop in the population size following implementation of the scenario, but here too the population recovers. The simulation for 80% of the mothers affected by an increase in their breeding threshold shows the same decline in the size of the population following implementation of the model (near year 1960; Figure 4.11c). In these three simulations however, the population does not (except for a 20% change in the threshold; Figure 4.11c, red) recover well. The population oscillates around a lower mean size, which is especially prevalent at an 80% increase for 80% of the mothers (Figure 4.11c, blue).

Implementation of the changes to the breeding threshold did not cause a significant sustained exponential decline to the population over time as is observed at Macquarie Island, but rather seemed to have more of an interannual effect on the population size. Although this may indicate that this hypothesis in isolation does not explain the observed population decline of southern elephant seals on Macquarie Island, we did continue further analyses on potential changes in the life history and breeding behaviour of the modelled individuals at 50% and 80% of the mothers affected by fecundity changes of 20%, 50% and 80% (*i.e.* populations of panels b, and c, of Figure 4.11). This showed that population dynamics and some individual emergent life history properties changed significantly depending on the severity of the implemented changes to the breeding threshold and the percentage of mothers who are affected (Table 4.3), compared to the baseline results.

The population dynamics, when looking at the percentage of juveniles and adults that make up the population, were significantly affected with fewer juveniles and an increase in the percentage of adults in the population, for all six scenarios (Figure A4A, B). There is a larger variation in the range of the juvenile proportion of the population with an increase in the breeding threshold of mothers indicating that over the selected time period (5 years in the model) there is an oscillation in the reproductive activity in the population. There was no significant difference in the survival of pups between the scenarios and the baseline model, and the survival of yearlings was reasonably similar across all simulations. Only scenarios with 50% of the mothers affected by 50% or 80% change showed a significant difference in

the yearling survival, although this variation was less than 5% either way, thus having little effect on the overall population (as is reflected in the population sizes; Figure 4.11).

The minimum age at first reproduction has not changed from the baseline (4.40±0.00; Table A3) for any of the simulations (Table 4.3). The generation time, however is significantly different from the baseline (9.49±0.03; Table A3) for all except one of the model simulations (Table 4.3). This shows that although on average the mother's first birth occurs as soon as her reproductive buffer has reached the breeding threshold, consecutive births are more difficult. This is explained by the significant loss of weight (or energy stores) that the mother experiences over the duration of her pregnancy, and particularly while she is weaning her pup (Goedegebuure et al., 2018, see also Figure 2 of) for the relative energy depletion during pregnancy). In the scenarios where the reproductive buffer has increased (by 20%, 50%, or 80%) it becomes significantly more difficult to reach this threshold at a young age (and after the first birth, when stores have been depleted).

Side effects of the mothers having a higher breeding threshold and associated lower breeding success (lower max number of births per mum; Table 4.3) are the significant increases in mean adult and maximum sizes. There is little difference in the mean size of juveniles between the baseline model and the scenarios, however the mean adult sizes become larger, and show a greater size-range, with the increasing changes in the breeding threshold (Figure A4C, D). This shows that when the seals (not solely the mothers, as some may not breed) are not putting resources into breeding, they allocate more energy to their own growth.

The fecundity of mothers was expected to be reduced through increasing their breeding threshold, by varying increments, however, although the maximum number of pups per mother (Table 4.3) was lower than the baseline (8.9±1.10; Tables A3) the overall fecundity increased with each scenario that had a higher breeding threshold. As the thresholds increased with the six analysed scenarios, the mean fecundity per age group did too (Figure 4.12), in other words; there are more pups produced per age group as the individuals get older and have stored more energy in their reproductive buffer. This is particularly the case for the scenarios where 80% of the potential mothers are affected by these increases in their reproductive thresholds.

Table 4.3. Population dynamics and emergent behavioural changes of the model with a scenario for the reduction of the fecundity of mothers where the reproductive threshold U_{cum} is increased by 20%, 50%, or 80% for 50% or 80% of the mothers. Results presented in the table are the means (± standard deviation) from the last five years of the simulations, where grey boxes indicate a significant difference (p <0.01) between the baseline model of Goedegebuure et al. (2018) and the scenario simulation. Results for lifespan of individuals exclude deaths of yearlings; proportions of juveniles exclude count of yearlings. * Indicates the change in population size is presented in Figure 4.11; ** indicates change in population dynamics is presented in Figure A4A, B; *** indicates change in juvenile and adult size is presented in Figure A4C, D.

	50% of mothers affected			**80% of mothers affected**		
	20% higher U_{cum}	50% higher U_{cum}	80% higher U_{cum}	20% higher U_{cum}	50% higher U_{cum}	80% higher U_{cum}
Population size *	1463±18	1463±17	1454±37	1478±7	1443±11	1412±13
Juvenile proportion **	37.49±1.75%	34.94±2.67%	32.16±3.78%	36.48±1.67%	31.55±1.42%	29.42±0.93%
Adult proportion **	42.52±0.97%	45.70±2.00%	47.56±2.80%	44.28±0.94%	47.85±1.51%	51.07±0.84%
Pup survival	98.01±0.50%	97.65±0.32%	97.78±0.20%	97.56±0.47%	97.12±0.50%	97.48±0.38%
Yearling survival	66.04±0.70%	63.33±0.25%	67.14±0.25%	62.47±2.71%	64.21±1.46%	69.03±0.79%
Age at first reproduction (yr)	4.40±0.00	4.40±0.00	4.40±0.00	4.40±0.00	4.40±0.00	4.40±0.00
Generation time (yr)	9.07±0.16	9.77±0.13	10.11±0.13	9.59±0.26	10.46±0.52	11.05±0.15
Juvenile age (yr)	3.68±0.13	3.36±0.20	3.04±0.15	3.48±0.12	2.98±0.21	2.90±0.07
Min adult age (yr)	5.10±0.03	5.06±0.05	4.97±0.13	5.08±0.07	4.99±0.06	4.92±0.07
Adult age (yr)	10.78±0.04	10.71±0.10	10.57±0.09	10.76±0.08	10.56±0.13	10.47±0.13
Lifespan (yr)	12.13±0.02	12.07±0.22	11.86±0.18	12.01±0.02	11.89±0.23	11.82±0.32
Max lifespan (yr)	26.71±2.47	25.24±0.60	25.43±1.22	25.07±0.78	26.28±1.55	25.76±0.67
Fecundity	0.28±0.01	0.31±0.01	0.32±0.01	0.29±0.01	0.33±0.18	0.36±0.01
Max number of births per mum	8.20±1.48	7.80±0.84	7.80±0.45	7.60±0.55	7.60±1.52	9.80±1.3
Juvenile size (cm) ***	167±0.76	167±1.00	165.35±1.03	167±0.75	165±0.80	165±0.57
Adult size (cm) ***	188±0.22	189±0.36	190±0.35	189±0.24	191±1.44	193±0.58
Max size (cm)	193±1.18	194±0.64	197±0.91	194±0.97	197±2.63	200±0.59
Relative food for (age >360 d)	0.73±0.02	0.73±0.02	0.74±0.03	0.73±0.02	0.75±0.01	0.78±0.01

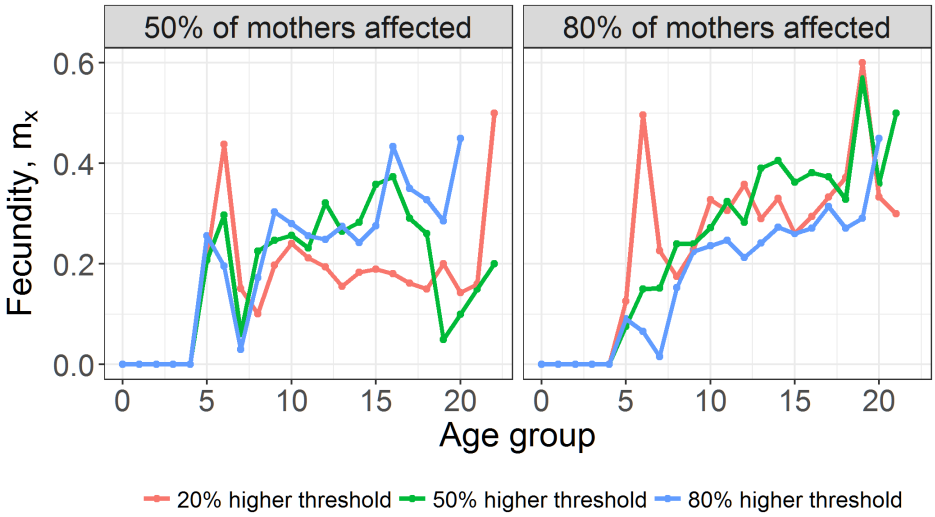

Figure 4.12. Comparison of fecundity over age classes for populations with scenarios for Hypothesis 3 - reduction in the fecundity of mothers m_x as presented in Tables A8-A13.

Hypothesis 4 - Density dependence

Running the model with a density dependency scenario, to see if the model could replicate the observed population decline at Macquarie Island, shows that the model can simulate the observed exponential decline. The modelled population shows an annual decline of -1.51% ($R^2 = 0.97$, Figure 4.13), compared to the observations of -1.46% ($R^2 = 0.87$ Hindell et al., 2017). The Pearson's product-moment correlation of the observations compared to the model was 0.89, with a Root Mean Squared Error (RSME) of 0.15. The mean population size of the model at the start of the simulation was 2337±38, which declined to 950±49 individuals over ∼70 years (Table 4.2, column 4). The simulation was run with a higher starting population to ensure that the decline could continue without the population collapsing before the end of the simulation. This affected only the overall size of the population, but not the underlying dynamics or emergent properties of the population. The exponential rate of change in the modelled population closely follows the observed population decline at Macquarie Island, between 1949 and 2015, although the model does not replicate interannual variation in the population size. This is due to the model following a long-term linear decline in resource availability (representing density dependence); *i.e.* every two years the decline in the resource availability was proportionally equal to the previous decline.

Both the mean juvenile age, and the mean age of transition (mean min adult age; Table 4.2,

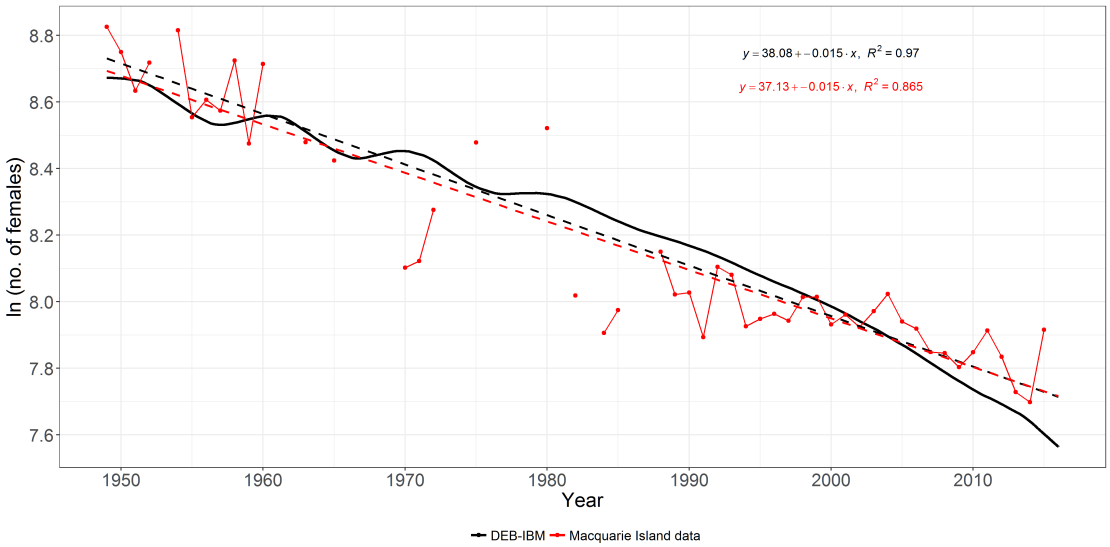

Figure 4.13. Comparison of log-normalised model population (black), using a smooth decline in food availability over 70 years, and the log-normalised counts from the Isthmus on Macquarie Island (red; 1949-2015). The modelled population results have been scaled to fit on the same time- and log- scale as the observations by adding 1930 years to the timeline, and though multiplication of the modelled individuals ($\times$ 2.5). The exponential rate of change of the model (black, dashed) is at -1.51% ($F = 1544_{(1,47)}$; p <0.01; $R^2 =$ 0.97), compared to the observations (red, dashed) at -1.46% ($F = 301.3_{(1,47)}$; p <0.01; $R^2 = 0.87$; see also Hindell et al. (2017)). The Pearson's product-moment correlation of the observations compared to the model was 0.89, with a Root Mean Squared Error (RSME) of 0.15.

column 4) were significantly higher in the simulation between 2010 and 2015 compared to the baseline, while there was no significant change in either the mean adult age, or lifespan (Table 4.2, column 4). The significant increases in the mean age of juveniles (from 3.85$\pm$0.07 to 4.82$\pm$0.37 years) and in the mean transition age (from 5.11$\pm$0.04 to 5.25$\pm$0.12 years; Table 4.2, column 4) are likely related to a number of changes happening to the population dynamics over time. The increase in mean juvenile age could be explained by an increase in the time it takes for juveniles to transition to adults, which would also explain the increase in transition age.

Another possibility would be that there are fewer pups transitioning to juvenile stage at later stages of the simulation, although this is unlikely due to the survival rate as the changes in the survival of yearlings were not significantly different from the baseline model (Table A14, Figure A5A). The overall rate of survival between age groups follows the same trend as the baseline, with a steep reduction in the number of individuals alive between birth and age

one. Thus, the variation in mean (transition) ages may be better explained by fewer pups being born. This is likely, as although the difference is not significant, the maximum number of births per mother decreased from 8.90±1.10 to 6.00±0.94 (Table 4.2, column 4).

The mean fecundity (0.25±0.01, and 0.28±0.00, respectively for the density dependence scenario and the baseline model, Table 4.2, column 4, and Table A3) and the maximum number of births per mother were significantly different from the baseline model to the end of the density dependence simulation; these changes can over time alter the population dynamics (*i.e.* a decrease in population numbers, and a significant decrease in the fecundity rate). The mean fecundity for each age group shows different responses between baseline model and the simulation, with lower overall fecundity of individuals between six and 20 years of age (Figure A5B, Table A14). The changes implemented with the density dependence scenario did not change the age of first breeding, with the first successful pregnancies by individuals between four and five years old, and the majority of first births between five and six years old.

4.4 Discussion

Using the implemented scenarios in the DEB-IBM we have shown that the model can reproduce the trend of the observed decline of the southern elephant seal population on Macquarie Island (except for the reduced fecundity hypothesis), however, the model did not reproduce the observed interannual variability of this decline. The emergent population dynamics changed from the baseline model results of Goedegebuure et al. (2018). Particularly the proportion of the population made up of juveniles and adults changed for every scenario, whereas the age of first reproduction or survival of pups barely changed. These changes, while at times significantly different from the baseline model, were often not unrealistic compared to the observations on Macquarie Island.

The scenarios

In the scenario for the effects of SAM-like climatic events with a perturbation amplitude of 0.985 the decline of the modelled population is reasonably matched with the observed changes in the southern elephant seal population on Macquarie Island, although the model does not represent the interannual variability of the data well. Periods with low resource availability in this scenario were too extreme to be realistic, as this affected fecundity of

females and the overall survival, especially for those individuals aged nine and up. In the ENSO-like climate scenarios with a perturbation amplitude of 0.744, the decline of the modelled population was less well matched; there was a strong oscillation in the size of the population over the duration of the model run and in the underlying dynamics, the emergent life histories, and in the individual breeding behaviour. Crocker et al. (2006) has shown the effects of severe El Niño Southern Oscillation (ENSO) events (including foraging difficulties, reduced survivorship, low reproductive success, and lower mass gains) on northern elephant seals *M angustirostris* to be due to factors such as a reduction in the abundance of prey, changes in the distribution of prey, or changes in oceanographic features.

The prey species of southern elephant seals are predominantly fish and squid (Vacqui-Garcia et al., 2015), both of which have very broad areas of distribution. Southern elephant seals have been found to change their diet seasonally, and in relation to their foraging range (Bradshaw et al., 2003); with squid-dominated diets following pelagic foraging in summer, and fish-dominated diets following winter foraging near the Antarctic continental shelf. El Niño Southern Oscillation events and other environmental occurrences affect these prey species at times positively, and at times negatively. While these variations in prey availability were represented in this model using the effective available food parameter, future versions of this model that make the model spatially explicit (as is discussed further in Chapter 5) could usefully implement explicit representations of prey fields.

While the means of the emergent properties are close to the observed life histories and breeding behaviour of females on Macquarie Island, there was excessive variation between years for the results compared to observations. One particularly significant variation in the emergent properties of the ENSO-like simulation was the change in the survival of yearlings (Figure 4.7) during the 'good' and 'bad' years. Yearling survival ranged between 15% and 85% over the duration of the model simulation. This followed a cycle where a bad year (around 30% survival) was followed by an intermediate year (around 60% survival) which was in turn followed by a few good years (around the expected 70% survival rate). The effects of years with low yearling survival cascade through the population and could possibly explain some of the other observed changes (such as the proportion of juveniles and adults within the population). While 'bad' years like this have been observed in the southern elephant seal population at Macquarie Island (*e.g.* Hindell, 1991, reports 2% survival of yearlings in 1965), and while smaller pups have less chance of survival than larger ones (*e.g.* McMahon et al., 2000), it is unlikely that such large interannual variation in yearling survival would occur at regular intervals. As yearlings were excluded from these analyses this does not explain the reduction in the mean and maximum lifespan of individuals; suggesting that older individuals

are also struggling in years of low food availability (see *e.g.* van den Hoff et al., 2014).

While the correlation between the observational data and the modelled results for the population decline was strong for both the SAM-like and ENSO-like simulations, the underlying population dynamics (particularly for the ENSO-like scenario) did not match observations. For both these simulations the 'bad' years in the climate cycle were too intense, with severe results. The SAM-like simulation was slightly more realistic, which indicates that the implemented sinusoidal variation was simplistic. Thus, as the simulation has shown that the decline in the population was reasonable and may be related to time-varying food availability, future work may focus on improving on the underlying calculations.

In the yearling survival scenario, where half of the yearlings were acquiring only half of their expected energy intake, the population dynamics were significantly different from the baseline model, as well as from the observations on Macquarie Island (see Table 4.2). While there was a sustained decline in the population size, similar to that observed on Macquarie Island, the mean ages of juveniles, adults, and the age at transition from juvenile to adult were significantly different from the baseline model. The mean age at transition was significantly lower than that of the baseline, with juveniles becoming physically mature almost six months sooner at the mean age of 4.66 ± 0.11 years old, and close to 1.5 years before the expected age of transition from observational data (Laws, 1956; Desprez et al., 2014). As the mean juvenile age decreased, the mean adult age and lifespan each increased by one year; suggesting that those juveniles who survive past their first year, are able to gain energy stores fast and become physically mature, sooner and may therefore represent the 'larger' yearlings with higher levels of survival (McMahon et al., 2000; McMahon and Burton, 2005).

The yearling survival reduced significantly in this scenario, as was expected from the reductions in energy intake. As the yearling survival reduced to a mean of 33% per year (see Figure 4.10), the mean fecundity of mothers increased. This was at first unexpected, however, this result is logical considering the reductions of energy intake for yearlings started at conception and thus the mothers are expending less energy to their offspring. This consequently leaves the mothers with larger reproductive buffers post-pregnancy and lactation, allowing them to stay above the cumulative breeding threshold. This allows mothers to have back-to-back pregnancies, which increases the overall fecundity, as well as the maximum number of pups per female. These changes in the mean fecundity and number of pups per female were, however, not enough to balance out the emergent survival rate of yearlings and maintain stability of the population. Given the differences in the modelled values from the observed we speculate that this scenario, in isolation, is unlikely to explain the observed population

decline of southern elephant seals on Macquarie Island.

With modifications made to the yearling survival scenario, the simulation could become more like observations; for example, the reduced energy intake by pups could be changed to only start at birth, or even after weaning. This would eliminate the effects of the mother's allocation of energy during pregnancy, and while lactating, and could reduce the fecundity rates, as well as reduce the number of pups born—who would then have a better chance of survival as they have been fed properly before they need to start supporting themselves.

In scenarios for a reduction in the fecundity of mothers, by implementing an increase in the breeding threshold, the expected fecundity of mothers increased (Table 4.3), which was unexpected. The fecundity by age group increased with an increase in the reproductive threshold, this showed that although the minimum age at first breeding did not change, there were fewer individuals who started breeding at this age. Those who did start breeding at this age struggled to continue with consecutive pregnancies as it took longer to get their reproductive buffer back up to the required threshold. This is not an unrealistic response; Desprez et al. (2014) showed that the cost of first reproduction at a young age could result in lower survival probabilities; Wilkinson and Aarde (2001); Fedak et al. (1996) discuss how smaller mothers expend comparatively more energy to bring up their offspring than larger mothers would. The remaining mothers, who chose not to breed at a young age, stored enough energy to surpass their reproductive buffer and were thus able to breed at least every three years. Thus, individuals who waited with their first pregnancy were more productive mothers, later in life. While this may seem counter-intuitive it highlights the cost of breeding at early ages, and the importance of self-preservation for the population as a whole (Viallefont et al., 1995; Desprez et al., 2014; Sanz-Aguilar et al., 2017).

A consequence of the change in breeding behaviour of the mothers was that as they were expending less energy to reproduction at an early age, their maturity thresholds increased at a greater rate. This also affected the age at which the juveniles transition to adult (younger than in the baseline model), and growth. In particular, the mean and maximum sizes of adults were significantly larger than that observed in the baseline model. This again shows that breeding comes at a personal cost to the mother, particularly in the early stages of adulthood (see also Hindell et al., 1994b; Fedak et al., 1996; Pomeroy et al., 1999). There is a difference in mean size of individuals in the different scenarios of almost six centimetres. While this difference seems small, it demonstrates that mothers are allocating their energy to growth and maintenance above reproduction. This re-allocation of energy expenditure could ultimately also be a driver in the population maintaining some stability as although

it iscostlier to start pregnancies early, the increased threshold for breeding does not affect more mature (and larger) individuals. Future applications of the model to explore changes in fecundity might usefully include an increase in the breeding failure rate for specific age groups.

To test if the hypothesis surrounding density dependence could be the driver of the observed exponential decline of southern elephant seals at Macquarie Island we implemented a scenario that lowered the carrying-capacity of the model. Taking into account the changes to the population (as a whole and on an individual level) the results of this simulation were realistic, however due to the inability of the model to accurately capture variation in the population size, this hypothesis in isolation does not explain the observed population decline of southern elephant seals at Macquarie Island. The modelled population showed an annual exponential decline of -1.51% which was similar to the observed decline at Macquarie Island (Figure 4.13).

With an implemented smooth decline in the carrying capacity of the model it was expected that the model was unable to capture the observed interannual variation. Had we chosen to develop a scenario which had a random element for the decline in the carrying capacity the results may have shown more of an interannual variation in population size. However, to limit the complexity of the model we chose not to do this, as we aimed to see how modifying the density dependence would play out in the model, and the model has given us reasonable results. Future work on the model could include adding this complexity to the scenario to get the results closer to the observations.

The results from the four scenarios suggest that multiple factors might be acting in concert; overlaying a periodic change in food with a reduction in yearling survival, or with density dependence, might replicate some of the variability. For example, van den Hoff et al. (2014) show that interannual variability in population growth rates was correlated with variability in the SAM in years prior to the observed change in the populations. The majority of the emergent population dynamics changed from the baseline model of Goedegebuure et al. (2018), and although these changes were significantly different, they are still within a reasonable range from the data collected at Macquarie Island.

Broader understandings and implementations

The implementation of the scenarios to the DEB-IBM show that while it is unlikely that a single driver can explain the southern elephant seal population decline, three of the four

drivers can force a population response that is broadly similar to the observed population. It is likely that either a more complex implementation of one of the scenarios, or a combination of multiple scenarios could produce a population response that is more similar to the observed decline, and thus one or all of these drivers may explain the population decline observed on Macquarie Island. Resource availability is likely to be a major factor in the population status of southern elephant seals, either through climatic variations at habitat and foraging sites (van den Hoff et al., 2014; Hindell et al., 2017) or through density dependence which may affect the resources available to individuals. This model indicates that a stable population is optimised around the availability of food, and having a surplus of food ('good' years) will only have a marginal impact as an increase in the available food will not make the individuals of the population consume more than they would optimally do. They may choose to breed more, although for a long-lived species this would take a long time to have any significant effect. In contrast, when food becomes limited ('bad' years) individuals can suffer immediately to the point of population collapse. We have shown that we have a model that can investigate the changes of energetics from climatic or other external factors on a large, colony breeding, marine mammal. We can relate external drivers (such as food availability) to population structure and can show how this may relate to the population decline of southern elephant seals on Macquarie Island.

This model is a newly available tool that can link external forcing to population outcomes through energetics by using the DEB-IBM framework. The model allows us to investigate population histories as well as potential population futures. Using the DEB-IBM that we have developed as a starting point it should be relatively straightforward to modify the parametrisation to simulate the three other southern elephant seal populations and use their similar energetics to look at the population structures at those locations and their drivers; for example we could investigate the different fecundity and breeding behaviour as observed on Marion Island (Pistorius et al., 2001, 2011) and tweak the model to suit different intrinsic or extrinsic factors to see what the effects would be on a different southern elephant seal population.

4.5 Conclusion and future works

While three of the fours scenarios demonstrated they could reproduce the observed trend in the population decline on Macquarie Island, none reproduced the interannual variability of the decline. This lack of variability is likely caused by our simplistic implementation of the

hypotheses. We deliberately chose simple forcing terms so that we could better understand the way the system was working. Our experiments have provided us with greater understanding of the workings of our DEB-IBM and show that it produced realistic changes in the population structure when an external forcing is applied. With further work we believe we could tweak the implementation of our scenarios to more closely reproduce the observed decline and use the DEB-IBM to answer ecological questions about the effects of scenarios (such as climate variability, or survival) on populations.

Long-lived species struggle with recovery, where slow recovery is attributed to reduction in adult female survival rates, yearling survival, and reproductive rates (including age at first reproduction) (Eberhardt, 2002). This was highlighted by the responses of the population in the model simulations for climate variability where large differences between 'good' and 'bad' years showed that the population struggled during continued 'bad' years. While the cyclical change in food availability could be a partial explanation for the observed decline in southern elephant seals at Macquarie Island (although not at severe amplitudes or durations) the set frequency in the simulations implemented in this model are overly simplistic and do not represent real-world climate variability. A more varying frequency and amplitude will likely result in a better match to the change in population. This would be an interesting scenario to run-in the model as the frequency and amplitude of climatic change is variable in the real world (*e.g.* Paolo et al., 2018, and references therein). To implement these variations, the population dynamics and emergent features would need to be closely followed and analysed as overly severe changes would result in a simulation that is no longer realistic. Furthermore, the overall simulation for density dependence was too linear in its responses to change (as is unsurprising considering the implemented change) and could become more realistic if the implemented density dependence were to incorporate some interannual variability. As with the climate hypotheses it is unlikely that there is little to no interannual variation in the changes (*i.e.* the implemented change should be different from year to year).

This model is a first DEB-IBM developed for a large (marine) mammal and demonstrates a new method of coupling detailed life history and breeding behaviour with energetics in an individual-based model (Goedegebuure et al., 2018). This DEB-IBM could prove to be useful for standardised development of IBMs as it facilitates analyses of life history contributions to population dynamics and could be implemented across species and ecological systems to analyses of the effects of, for example, environmental changes to both individuals and populations. For future testing of hypotheses of the potential drivers behind the population decline at Macquarie Island with this model we recommend implementing a combination of the hypotheses tested here. Particularly we recommend combining climate variations (or

density dependence) and yearling survival scenarios, and to change the yearling survival to a more realistic energy intake limitation that starts at birth, or potentially post-weaning.

Better results for testing hypotheses could arise if this model is implemented for a number of populations for comparison. This would, for example, allow us to see what the effects of the initial parameters are on the whole of the model—and to see if the populations then respond the same to the implemented changes to test the hypotheses, see for example the comparison of southern elephant seals on Marion and Macquarie Island by McMahon et al. (2005a). Implementation of the model to different populations, or different species for that matter, could highlight factors that would benefit continued observations in existing populations, or potentially raise features for new observations.

Chapter 5

Synthesis and future work

5.1 Synthesis

Ecosystems are affected by changes in climate, which have escalated in recent years. The need for assessing ecosystem status and trends is highlighted by these changes, and the affected biological, ecological and social systems. Through a combination of observations and modelling methods we can use an ecosystem based approach to management of these systems (Chapter 1). This project started with research on the current representations of higher trophic level species in end-to-end ecosystem models (as highlighted in Chapter 2). We showed that many end-to-end ecosystem models had limited representations of higher trophic level (non-fish species) predators.

To examine the impact of limited representations of higher trophic level species in ecosystem models, we developed a simple ensemble of qualitative network models (for more detail on qualitative network models, see Dambacher et al., 2002; Melbourne-Thomas et al., 2012) for a Southern Ocean foodweb. We demonstrated that differing levels of complexity in representation of top predators led to notably different outcomes. This has been demonstrated previously (Gårdmark et al., 2013), through an ensemble of models with varying ecological assumptions, for the Eastern Baltic cod *Gadus morhua callarias*. While maintaining an ensemble of models is significantly more expensive than a single model; in circumstances where the effect of changes to model structure are unknown, but likely to be significant, an ensemble where the members have different realisations of key components (such as higher predators or climate forcing) is an effective way of quantifying this impact.

We examined the current methods for representations of apex predators (seabirds and marine mammals) in ecosystem models, and considered where improvements could be made.

Chapter 5

Recognising the importance of bioenergetics and the effects of resource availability for ecosystem based (fisheries) management, we opted to expand on DEB-IBMs and develop a model that could combine the energetic intake and expenditure as well as the complex life histories, breeding and foraging behaviour of a colony breeding marine mammal, the southern elephant seal *Mirounga leonina* (Chapter 3).

This modelling framework combines the deterministic approach of dynamic energy budget theory with the stochasticity of individual based modelling. This incorporates the individual's assimilation and energy use for growth, maintenance and reproduction, with individual and multi-level interactions as well as system behaviour (*i.e.* ecosystem dynamics). The DEB-IBM, a first developed for a large (colony breeding, marine) mammal, projected a stable population while maintaining realistic population dynamics and structure based on emergent life history traits, breeding behaviour and energy use.

The data used for the development of this model came from longitudinal studies on the population of southern elephant seals at Macquarie Island. This population has been in decline for the last 60 years (McMahon et al., 2005b; Hindell et al., 2017); the drivers behind this decline are unknown. Hypotheses regarding the driver behind the population decline postulate female mortality, breeding success, yearling survival and environmental changes at foraging grounds. We used the model to investigate hypotheses of potential drivers behind the southern elephant seal population on Macquarie Island by implementing scenarios of climate variability, yearling survival, fecundity, and density dependence (Chapter 4).

The model simulations showed that there were significant differences in the population following the implementations of the four scenarios. The emergent features of the population suggested that a combination of the scenarios could be used to answer ecological questions about potential changes to populations. While three of the fours scenarios demonstrated they could reproduce the observed trend in the population decline on Macquarie Island, none reproduced the interannual variability of the decline. This lack of variability is likely caused by our simplistic implementation of the hypotheses; thus with further work we believe we could tweak the implementation of our scenarios to more closely reproduce the observed decline and use the DEB-IBM to answer ecological questions on how intrinsic or extrinsic changes can affect populations.

5.2 Future directions

This DEB-IBM for southern elephant seals is the first of its kind developed for a large (colony breeding, marine) mammal. It simulates a stable population and has the ability to examine the affects produced by altering a range of internal and external drivers, such as fecundity, yearling survival, and climate variability. Nonetheless, this model has some limitations that should be explicitly acknowledged. This DEB-IBM is not spatially resolved, it does not specifically model males, and relies on a single, scaled, food source. Including males in the model, as well as developing a dynamic prey field, and spatially resolving the model would add considerable complexity to this DEB-IBM. Such increases in complexity should be carefully considered, as discussed in Chapter 2 (and see Fulton et al., 2003). Consequently, these limitations were carefully considered during the development of the model, and these three factors were deliberately excluded. For future developments, however, these would be interesting additions to the model, taking into account that the added complexity needs to be weighed up against the added benefits (Fulton et al., 2003).

Including males in the model

The justification for only including females in this DEB-IBM was based on the importance of female southern elephant seals in the population, in contrast to males. Adult male seals make up only ∼36% of the population and survive to approximately 15 years of age (compared to 23 years of age for females, see Table A2). Additionally, with southern elephant seals being harem breeders (one dominant male to dozens of females), only around 8% of adult bulls sire pups in any given year (based on the number of males over the age of 9, and the number of pups born in that year; see Chapter 3). If the DEB-IBM were to be used to collect information on the energetic requirements of a population, however, including males in the model would be beneficial.

New parameters need to be included in the model as there are significant differences between male and female southern elephant seals. These seals exhibit significant sexual dimorphism, with males weighing up to 3000 kg, and females up to 800 kg (*e.g.* Laws, 1953; McLaren, 1993), and somatic growth ends a year later for males than for females (Laws, 1956; Desprez et al., 2014). For the DEB component of the model, these parameters include addition of male specifics for somatic and maturity maintenance coefficients, $\dot{k}_M$ and $\dot{k}_J$, respectively; shape coefficient δ_M; effective food availability f_{eff}; volumetric structural lengths at birth L_b,

weaning L_x, puberty L_p, and ultimate length L_m; maturity thresholds at birth E_H^b, weaning E_H^x, and puberty E_H^p; as well as ageing parameters. For the IBM component this includes adding durations for fasting and foraging, as well as the timing at which males come to land for breeding. These durations and times change depending on the age and status of the males (Carrick et al., 1962); for example young males will leave the breeding colony before the dominant bull. To implement the DEB parameters we recommend using DEBtool (www.debtheory.org/) to collect the required values.

Making the model spatially explicit

The DEB-IBM contains a non-spatial environment represented by an effective food availability for each individual. Competition was added to the model to reduce overestimating food availability. The implemented competition term ensures that food availability is dependent on the size of the population; thus as the population increases past a set carrying capacity, the effective food availability reduces. Making the model spatially explicit could improve the accuracy of the energy intake and expenditure of individuals, especially when taking into account the different foraging trips over winter (low productivity) and summer (high productivity) (see O'Toole et al., 2015), which could also impact survival (as discussed in Chapter 4. This would be achieved by replacing the absolute and effective food availability, f_{a} and f_{eff}, respectively, with a number of prey dynamics parameters from DEB theory. These include prey density X for each patch (or grid cell) within the model (see also Wilensky, 1999; Kooijman, 2010b; Martin et al., 2012); the (half) saturation coefficient (K in Kooijman, 2010b); the surface-area-specific maximum ingestion rate $\{\dot{J}_{XAm}\}$, and; the specific searching rate $\{\dot{F}_m\}$ (Kooijman, 2010b; Martin et al., 2012, and references therein). Considering that seals forage in a three dimensional space, diving behaviour (McConnell et al., 1992; Labrousse et al., 2017), and associated energetic costs, could be added.

The prey specific parameters would need to be adjusted based on the target prey species and their energetic content. Southern elephant seals consume a combination of fish and squid species, which varies depending on the season and foraging location (Bradshaw et al., 2003). Additionally, as discussed in Goedegebuure et al. (2018), adding males to the model could add valuable detail as the males have different foraging patterns and may thus be affected differently by environmental changes affecting prey field than females (Labrousse et al., 2017).

Inclusion of a more detailed prey field could modify the mortality rates of the whole popu-

lation. While first year survival of the modelled population was similar to that observed on Macquarie Island, this trend did not continue (see Chapter 4, Figure 4.1). Individual mortality rates in the model are split at the one-year age group (pup, and non-pup). This was done as there was limited data available surrounding the reasons of pre-mature death of southern elephant seals on Macquarie Island. Thus, forcing individual survival would be artificial and would have been done without understanding the reasoning behind the survival rates per age group. This could be further developed in a model that could explicitly represent survival by age in connection with different hypotheses (*e.g.* for predation, disease, the effects of changes in physiology and metabolism on survival).However this would require more in depth and *in situ* studies of these species, such as tracking studies."

Adapting the model to other species

We have shown how this DEB-IBM can be used to represent a large colony predator and suggest that the template for this model could be used for other species. The simplest change would be to adapt the model to marine mammals with similar breeding behaviours (*i.e.* species that haul-out to breed for a selected period, and in which the mother provides for the pup), such as land breeding Fur seals *Arctocephalus spp* (Guinet et al., 2001), or ice-breeding seal species, such as Weddell *Leptonychotes weddellii* or Crabeater seals *Lobodon carcinophagus* (Southwell et al., 2012, and references therein). Adaptations for the model for whales would require implementation of longer fasting periods over winter months, and excessive feeding during summer months (*e.g.* Leaper et al., 2006). Adaptation for seabirds would need to include parameters for egg-laying, regurgitation, as well as role-swapping of male and female birds (*e.g.* Southwell et al., 2017).

An interesting seabird species to be modelled could be the Adélie penguins *Pygoscelis adeliae*. These seabirds have been an indicator species for the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (see *e.g.* Emmerson and Southwell, 2011; Southwell et al., 2017). Changes have been observed in the global population, with declines on the west Antarctic Peninsula and increases in population on East Antarctica (Lynch and LaRue, 2014). Concurrently, it would be interesting to implement this model to two (or more) different species who breed in similar regions, but respond differently to environmental pressures.

The model could, for example, be adapted to Adélie and gentoo penguins *Pygoscelis papua* who both breed at the South Orkney Islands. Adélie penguins are an ice-dependent circum-

Antarctic continental species and have few populations on more northerly islands (Forcada et al., 2006; Emmerson and Southwell, 2011). Gentoo penguins on the other hand are a more sub-Antarctic species with few colonies on southernmost islands (Lescroël and Bost, 2005; Forcada et al., 2006). On the South Orkney Islands, the Adélie penguins are at the northern most limit of their habitat range, where the gentoo penguins is at their southernmost limit. Here the Adélie penguin population has declined over the past 26 years, whereas the gentoo penguin population has increased (Forcada et al., 2006) in response to climate variation.

Implementing scenarios relating to temperature increase and consequent reduction in sea ice extent to DEB-IBMs for each of the species could show the differences in emergent features (such as changes in energy intake and expenditure, breeding behaviours and survival). Considering the differences in habitat requirements between the two species, this implementation of the DEB-IBM could highlight individual responses and subsequent consequences of environmental effects on the species. This could be used to answer ecological questions about potential effects of climate variation on these and other (similar) populations such as the sub-Antarctic chinstrap penguins *Pygoscelis antarctica*, or ice-dependent emperor penguins *Aptenodytes forsteri*.

Implementing the model into end-to-end ecosystem models

End-to-end ecosystem models, or whole-of-system models, are developed for a multitude of reasons, including the assessment of trophic functioning and interactions in larger ecosystems (*e.g.* Guénette et al., 2014; Fiechter et al., 2015, 2016); to analyse environmental influences on ecosystem dynamics (*e.g.* Maury et al., 2007a,b; Maury, 2010), or; to assess the effects of fisheries on foodwebs (*e.g.* Gurney et al., 2014). These end-to-end ecosystem models encompass entire ecosystems, and include all trophic-levels, at varying levels of detail (*e.g.* Fulton et al., 2003; Murphy and Hofmann, 2012; Gray et al., 2014; Fulton et al., 2015). The need for understanding trophic interactions has recently been demonstrated; specifically for including humans and predator species at high trophic-levels, and incorporating regional variability in models—particularly where used for management purposes (Hobday et al., 2013, 2015; Maury et al., 2013).

Currently there is a gap in the inclusion of detailed representations of seabirds or marine mammals in end-to-end ecosystem models which include the life histories, breeding behaviour and energetics (Goedegebuure et al., 2017). This is despite of the fact that these species play important roles in their respective ecosystems (*e.g.* Sala, 2006; Constable et al., 2014;

Kiszka et al., 2015). We suggest that our DEB-IBM could be implemented into end-to-end ecosystem models to replace higher trophic-level species that are represented using closure terms in these models.

5.3 Concluding remarks

This thesis presented a first DEB-IBM for a colony breeding marine mammal. This model for southern elephant seals produced a biologically realistic, stable population and can be used to project effects of intrinsic and extrinsic changes through analyses of behaviour and energy use. We have shown that the model can be used to examine hypotheses regarding population change, as the model produced realistic responses in populations when an external forcing was applied. We have shown that DEB-IBMs can be used to represent the complex life histories of southern elephant seals. Consequently this model can give us a better understanding of potential drivers behind changes in populations and could highlight factors that would benefit continued observations in existing populations.

The development of this model, and the implementation of the scenarios to test hypotheses behind the population decline has shown a process on how southern elephant seals could be used as sentinels (in line with Hindell et al., 2003; Constable et al., 2014, 2016). The model can be used to investigate drivers of population change while tracking individual as well as population dynamics. This model can advance the detailed representations of higher trophic-level predator species and has potential to add these detailed representations to end-to-end ecosystem models. On its own, this DEB-IBM can be used to test the organism's response to climate change and thus can assist conservation management.

Appendices

A1 Survey of commonly used approaches for the representation of top predators in end-to-end ecosystem models

Table A1. Survey of commonly used approached for the representation of top predators in end-to-end ecosystem models — explaining the design and use of each model, the predators included, and the detail of their representation or the closure methods used in the model. The models selected are all considered end-to-end ecosystem models with varying levels of complexity in predator representations. References for each model are given with the model name.

Model name	Model design	Predators	Predator representations
Ecopath with Ecosim Christensen and Walters (2004); Christensen et al. (2008)	Integrated software package combining static, mass balance approach (Ecopath) with dynamic modelling (Ecosim).		Ecopath generally includes two mortality terms for formulation of total production rate (see Eq. 1; Christensen and Walters, 2004) for prey species – which include a predation tem (see Eq. 3; Christensen and Walters, 2004) and 'other mortality' (see Eq. 2; Christensen and Walters, 2004, a catch all term for mortality not elsewhere included).
Ecopath model for the Prince Edward Archipelago, Southern Ocean Gurney et al. (2014).	Describes the ecosystem using a static, mass balance approach assuming a steady state, closed ecosystem.	16 predator groups, see Table 1 in Gurney et al. (2014). ▪ Orcas *Orcinus orca* ▪ Seals (3 individual species) ▪ Penguins (4 individual species) ▪ Albatross (5 individual species) ▪ Giant Petrels (2 species) ▪ Prions and petrels (14 species) ▪ Sharks and rays (6 species)	Predators were represented using species aggregated into functional groups, based on size, habitat use, diet, and fisheries/conservation considerations.

Table A1: Continued

Model name	Model design	Predators	Predator representations
Ecopath with Ecosim model for the Banc d'Arguin and the Mauritanian shelf, North Atlantic Ocean. Guénette et al. (2014)	To assess the trophic functioning of a larger ecosystem, including low, mid and high trophic levels.	31 predator groups, see Table 1 in Guénette et al. (2014). We only include the first two groups as top predators: ▪ Marine mammals (20 species): ▪ Orcas ▪ Monk seals ▪ Harbour porpoises *Phocoena phocoena* ▪ Dolphins, pilot whales, pigmy sperm whales (14 species) ▪ Beaked whales (3 species) ▪ Birds (30 species) ▪ Breeders (15 species) ▪ Waders (15 species)	As above
SEAPODYM (Spatial Ecosystem And Population Dynamics Model) for the Pacific Basin Lehodey et al. (2003); Lehodey (2004); Lehodey et al. (2008); Dragon et al. (2015)	Combined physical-biological interaction model.	Skipjack tuna *Katsuwonis pelanis* Yellowfin tuna *T. albacoares* Bigeye tuna *T. obesus* Albacore tuna *Thunnus alalunga*	Tuna are represented using age-structured populations ▪ Juvenile stage mortality terms: ▪ Natural (predation and starvation) ▪ Fishing ▪ Adult stage mortality terms: ▪ Fishing

Table A1: Continued

Model name	Model design	Predators	Predator representations
OSMOSE (Object-oriented Simulator of Marine Ecosystem Exploitation) for the Southern Benguela ecosystem (South Africa) Shin and Cury (2001, 2004)	Multi species individual-based model (IBM) for high trophic levels.	Piscivorous fish Non-piscivorous fish Birds Marine mammals	Piscivorous and non-piscivorous fish within IBMs: ▪ Super individuals *sensu* Scheffer et al. (1995) ▪ Species aggregates (age & taxonomy) ▪ Constrained by carrying capacity (prey biomass) Birds and marine mammals: ▪ Global variables/parameter
Coupled ROMS-$N_2P_2Z_2D_2$-OSMOSE model for the Southern Benguela ecosystem (South Africa). Travers-Trolet et al. (2014a,b)	Combined ROMS (Regional Ocean Modelling System; hydrodynamic model), $N_2P_2Z_2D_2$ and OSMOSE end-to-end ecosystem model.	Piscivorous fish Non-piscivorous fish	Fish as per OSMOSE (above). Additional mortality terms: ▪ Natural mortality (starvation, disease, senescence) ▪ Predation by higher trophic levels; (see eq. 5 in Travers-Trolet et al., 2014b) ▪ Fisheries dependency term

Table A1: Continued

Model name	Model design	Predators	Predator representations
Coupled NEMURO end-to-end ecosystem model for the California Current (North America). Fiechter et al. (2015); Rose et al. (2015); Fiechter et al. (2016)	Combined ROMS, NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography) NPZ (nitrogen, phytoplankton, zooplankton) sub-model with an IBM for higher trophic levels to understand trophic interactions and effects on habitat utilisation. Recent further development of the model includes a detailed IBM for male California sea lions (Fiechter et al., 2016). Here, tuna have been removed from model simulations, and detritus is added to the NPZD sub model.	Inshore anchovy Offshore sardine Albacore tuna Fishing fleet sub-model California sea lion	Anchovy and sardine populations represented using super individuals in IBMs California sea lions represented using detailed IBMs which include bioenergetics through a mechanistics dynamic model *sensu* Lavigne et al. (1986) to track energy use for production and maintenance. Additional mortality terms: ▪ Natural mortality (starvation, senescence) ▪ Predation by Albacore tuna (simplified IBM for predation on sardines and anchovy) ▪ Fisheries mortality (separate agent-based sub-model for predation on sardines only)

Table A1: Continued

Model name	Model design	Predators	Predator representations
APECOSM (Apex Predators Ecosystem Model) for pelagic ecosystems, and APECOSM-E (Estimation). Maury et al. (2007a,b); Maury (2010); Dueri et al. (2012b,a)	APECOSM is developed to model environmental influences on marine ecosystem dynamics. It represents the flow of energy through an ecosystem using dynamic energy budget theory for open ocean pelagic ecosystems in combination with a size-spectrum approach. APECOSM-E is a single species version for parameter estimation.	APECOSM: ▪ Skipjack tuna ▪ Yellowfin tuna ▪ Bigeye tuna ▪ Albacore tuna APECOSM-E: ▪ Skipjack tuna	Tuna are represented using dynamic energy budget (DEB) theory (Kooijman, 2010b). Additional morality terms: ▪ Natural (starvation, instantaneous, non-predatory) ▪ Fishing
Atlantis (Fulton et al., 2004)	The Atlantis modelling framework combines physical, biological and fisheries sub-models.		Atlantis allows for representations of mid- to high trophic levels through either aggregates or they can be resolved at species level.
Atlantis model for South East Australia Fulton et al. (2007); Audzijonyte et al. (2014a,b)	Fulton et al. (2007) designed the model for fisheries management strategies. Audzijonyte et al. (2014b) adjusted the model to compare life-history changes and fishing effects on ecosystems. Audzijonyte et al. (2014a) used the model to analyse stock recovery changes and the impacts from changes in body sizes of fish.	Predator species included: ▪ Seals ▪ Sea lions ▪ Dolphins ▪ Whales ▪ Orcas ▪ Large predatory fish	The vertebrate predators were represented through age structures. Many fish species were aggregated where possible - except those that were of particular interest relating to the fisheries. Seals, dolphins and baleen whales were grouped. Sea lions and orcas each had their own model components.

Table A1: Continued

Model name	Model design	Predators	Predator representations

Atlantis model for the California Current, North America.
 	
Brand et al. (2007); Horne et al. (2010); Kaplan et al. (2014)
	Brand et al. (2007) developed the model to test potential policies and management tools for balancing competing species and fisheries trade-offs. Horne et al. (2010) adjusted the model to allow for guiding ecosystem based management by increasing understanding of complex dynamics of marine ecosystems and how humans fit into this system. Kaplan et al. (2014) adjusted the model to address questions relating to ocean acidification and ecosystem-based management of forage fish.	Predator species included:
		▪ Birds
		▪ Separated in Kaplan et al. (2014):
		  ▪ Benthic and pelagic feeders
		  ▪ Pelagic feeders
		  ▪ Migrating seabirds
		▪ Seals
		▪ Separated in Kaplan et al. (2014):
		  ▪ California sea lions
		  ▪ Harbour seals *Phoca vitulina*
		▪ Orcas
		▪ Baleen whales
		▪ Toothed whales
		▪ Separated in and Horne et al. (2010); Kaplan et al. (2014):
		  ▪ Small cetaceans
		▪ Sea otters *Enhydra lutris*
			Vertebrates were represented by age classes (which were set according to life stage, not necessarily age). From the original model, the birds were separated between migrating, surface and diving birds as these have different life histories and could not be combined.
			
			Linear and/or quadratic mortality terms were used for all trophic levels where predation terms were not sufficient to generate reasonable age structures or cap growth.

Table A1: Continued

Model name	Model design	Predators	Predator representations

InVitro for Ningaloo-Exmouth region, Western Australia.
 	
Gray et al. (2006); Fulton et al. (2011); Gray et al. (2014); Fulton et al. (2015)
	Whole-of-system model combining biophysical, socio-economics, industry, management and monitoring and assessment sub-models for Ningaloo-Exmouth region, Western Australia.	▪ Turtles
		▪ Emperor fish
		▪ Other fish
		▪ Seabirds
		▪ Manta rays
		▪ Sharks
		▪ Whales
		▪ Whale sharks *(Rhinocodon typus)*
		▪ Dolphin species
		▪ Dugongs *(Dugong dugong)*
			Predators are represented as:
			▪ Metapopulations
			  ▪ Egg and juvenile turtles and emperor fish
			  ▪ Other fish
			  ▪ Seabirds
			▪ IBMs
			  ▪ Adult turtles and emperor fish
			  ▪ Manta rays
			  ▪ Sharks
			  ▪ Whales
			  ▪ Dolphins
			  ▪ Dugongs
			
			Additional mortality terms:
			▪ Natural (density dependent, random or exponential decay, senescence and starvation)
			▪ Human induced (includes fishing, catastrophes and poisoning)

A2 Process of parameter estimation using DEBtool

Appendix A2

I used DEBtool 8.3.0.532, operating within Matlab R2014a. This version was downloaded on 19-07-2016 from http://www.debtheory.org/, for add_my_pet (AmP). Since the initial development of this model, and the dowloads of the required tools and quides, DEBtool (and now AmP) have undergone significant changes.

The below outlines the final modifications that were made to the generic add_my_pet downloads for DEBtool. The full process of deriving accurate DEB parameters for the current version of DEBtool and AmP are explained on the following website http://www.debtheory.org/wiki/index.php?title=AmP_estimation_procedure. Specifically, a detailed explanation of the process that was used here for the parameter estimation and setting the initial parameter values for DEBtool are now found here http://www.debtheory.org/wiki/index.php?title=Setting_initial_parameter_values. This process needs to be run through numerous times to match some 15 parameters in the initial settings.

The download for DEBtool comes with many Matlab scripts, with four scripts that are used as 'user defined files for your selected species' (http://www.debtheory.org/wiki/index.php?title=Starting_an_estimation_for_a_new_species): 1. 'mydata_Mirounga_leonina',
2. 'pars_init_Mirounga_leonina', 3. predict_Mirounga_leonina', and 4. 'run_Mirounga_leonina'

1. 'mydata_Mirounga_leonina' stores the initial data that is available for the species.
    a. I changed the age at birth from 220 days to 226 days according to Laws (1984)
    b. Temperature parameter was set according to Little (1995), 38.1°C
    c. Age of sexual maturity was changed following Desprez et al. (2014). The age at sexual maturity females, start of breeding, was at age 3 (or 1095 days)
    d. I added data for the lengths for birth (110 cm), weaning (125 cm) and puberty (180 cm) for southern elephant seals.
    e. Weights at birth (45 kg) and weaning (117 kg) changed following cited references in text.
2. 'pars_init_Mirounga_leonina' contains a function that estimates initial parameters for DEB. The modification of the parameters below resulted from numerous tests of the resulting parameters from 'run_Mirounga_leonina' – which are the final parameters used in the DEB-IBM for southern elephant seals.
    a. I modified the zoom factor for females (z) from 46.98 to 66

   b. I modified the energy conductance (v) from 0.07549 to 0.065
   c. I modified the allocation of fraction to soma (kap) from 0.69 to 0.79
   d. I modified the specific cost for structure (E_G) from 7971 to 8400
   e. I modified the maturity at birth (EH_b) from 7.730e7 to 2.81e7
   f. I modified the maturity at weaning (EH_x) from 7.944e7 to 6.5e7
   g. I modified the maturity at puberty (EH_p) from 1.956e8 to 1.795e8
   h. I modified the Weibull aging acceleration (h_a) from 9.403e-13 to 9.3e-12
   i. I modified the shape coefficient (del_M) from 0.179 to 0.235

3. 'predict_Mirounga_leonina' uses the above two scripts to predict the DEB parameters for the chosen species
   a. I included a calculation for the wet weight at puberty (Ww_p)
   b. I included lengths at birth (Lw_b), weaning (Lw_x) and puberty (Lw_p')
4. 'run_Mirounga_leonina' uses the above three scripts to output all DEB parameters for the chosen species, here for southern elephant seals
   a. I changed the *estim_options('pars_init_method', 2)*; so that initial parameters can be changed through pars_init_Mirounga_leonina.

For estimating the confidence in parameter values I chose to perform manual sensitivity analyses by using the DEBtool results as initial values. The DEB parameter values, along with the IBM parameter values for southern elephant seals were included in the DEB-IBM. The sensitivity testing of the parameters was done using a combination of tests using the DEBtool scripts and the DEB-IBM. I compared the observables from the model (e.g. transition ages, sizes, breeding behaviour) to observations of real populations. Changes to DEB parameter values meant that the DEBtool scripts were run again to ensure no un-observable parameters were changed (e.g. energy conductance, energy investment ratios, or assimilation rates). The parameters were varied and tuned so that the observables from the model matched existing data from southern elephant seal populations.

A3 Life table of southern elephant seals at Macquarie Island

Appendix A3

Table A2. Comparison of survival rates and relative numbers of males and female southern elephant seals on Macquarie Island derived from capture-mark-recapture studies. Hot-iron brands were used to individually and permanently mark seals. A combination, alpha-numeric brand was applied in different orientations on the seals to uniquely identify each individual (Chittleborough and Ealey, 1951; McMahon et al., 2006b) over long periods (Hindell and Little, 1988) without any deleterious life-history affects (McMahon et al., 2006a, 2007, 2006b; van den Hoff et al., 2004). Maximum observed age of males is 15 years old, and females is 23 years old.

Age	Male survival	Number of males	Female survival	Number of females
0	1	2000	1	2000
1	0.671	1342	0.696	1392
2	0.534	1068	0.568	1136
3	0.438	876	0.463	926
4	0.361	722	0.387	774
5	0.275	550	0.335	670
6	0.201	402	0.267	534
7	0.151	302	0.208	416
8	0.118	236	0.166	332
9	0.088	176	0.138	276
10	0.058	116	0.114	228
11	0.035	70	0.087	174
12	0.02	40	0.064	128
13	0.008	16	0.048	96
14	0.006	12	0.037	74
15	0.002	4	0.029	58
16			0.022	44
17			0.018	36
18			0.014	28
19			0.011	22
20			0.008	16
21			0.006	12
22			0.005	10
23			0.004	8

A4 Figures for Chapter 4: Using the DEB-IBM to test hypotheses on the potential drivers of the observed population decline in southern elephant seals at Macquarie Island

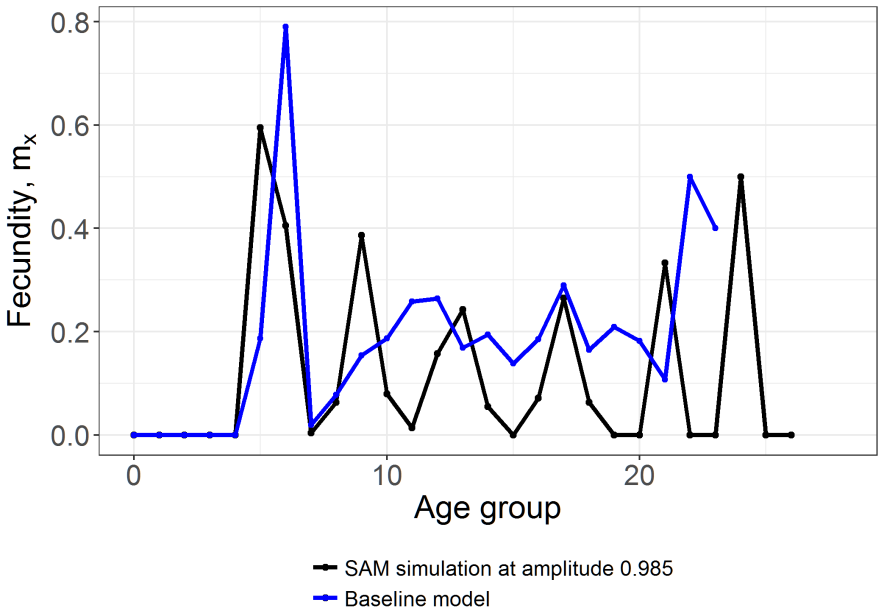

Figure A1. Comparison of lifetime fecundity m_x for the baseline model (blue) and Southern Annular Mode (SAM-like) simulation (black). Full life table data is presented in Tables A4 and A5.

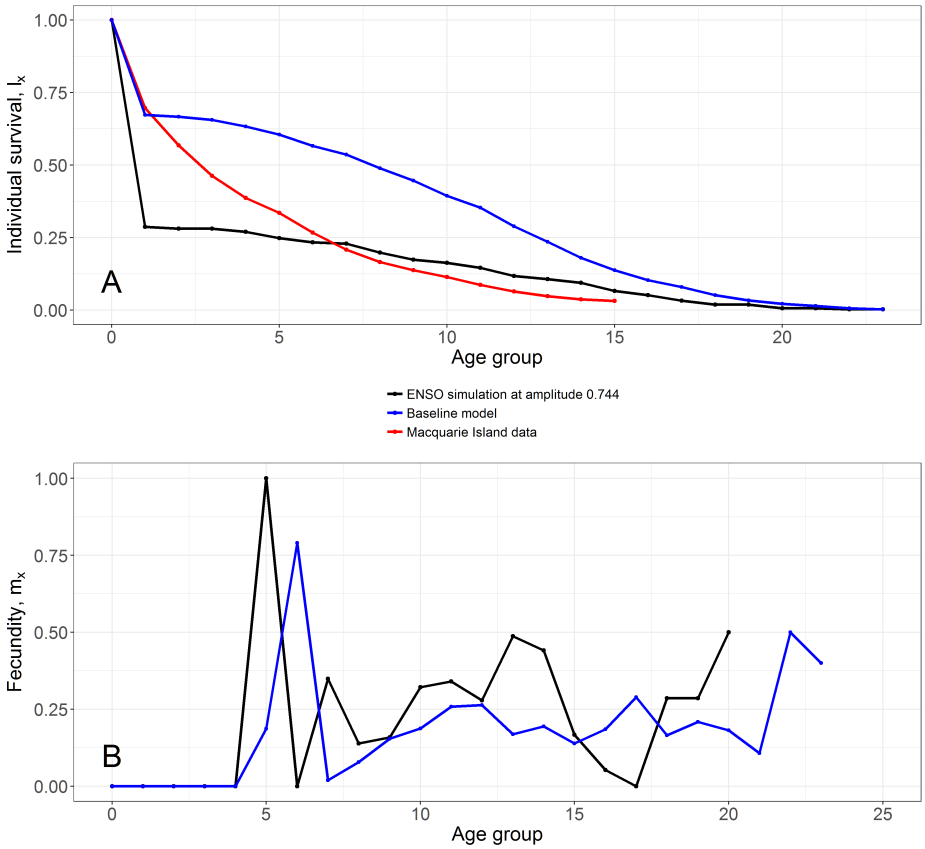

Figure A2. A) A comparison of the proportion of individuals surviving from one age group to the next l_x, in the baseline model (blue), during El Niño Southern Oscillation (ENSO-like) simulation (black) and Macquarie Island observations (red). B) Comparison of lifetime fecundity m_x for the baseline model (blue) and El Niño Southern Oscillation (ENSO-like) simulation (black). Full life table data is presented in Tables 4.1, A4 and A6.

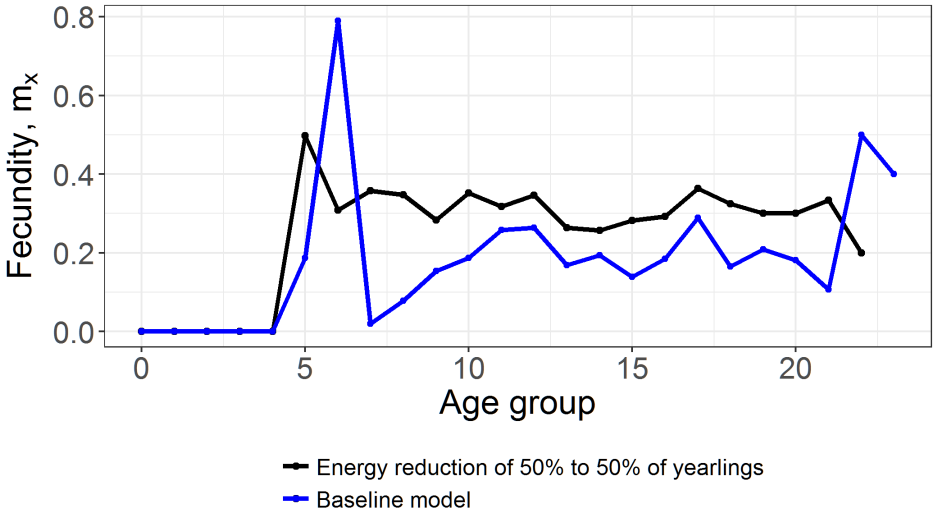

Figure A3. A comparison of the lifetime fecundity m_x for the baseline model (blue) and the simulation of a 50% reduction in energy intake by 50% of yearlings (black). Full lifetable data is presented in Table A7.

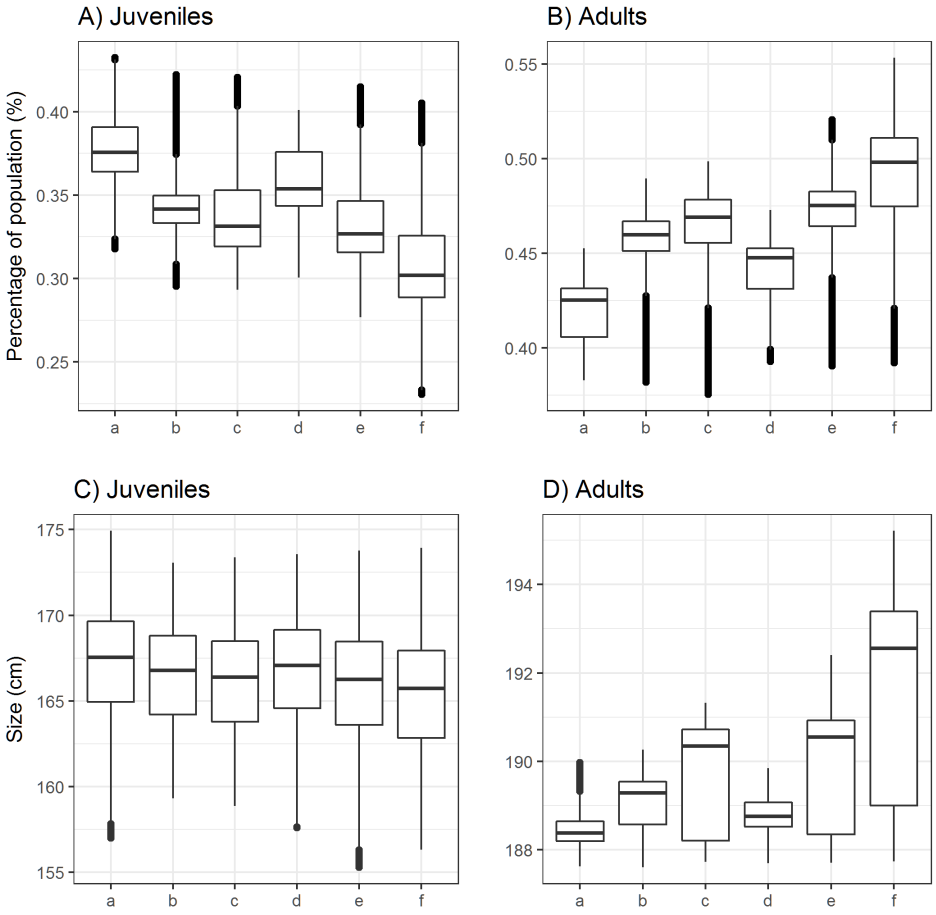

Figure A4. Population dynamics for populations with scenarios for Hypothesis 3 - reduction in the fecundity of mothers. Plot A) shows the mean percentage of juveniles in the population; plot B) shows the mean percentage of adults in the population; plot C) shows the mean juvenile size (cm); plot D) shows the mean adults size (cm). The x-axis labels of all plots refer to: a, 50% of mothers affected by a 20% increase in the breeding threshold; b, 50% of mothers affected by a 50% increase in the breeding threshold; c, 50% of mothers affected by a 80% increase in the breeding threshold; d, 80% of mothers affected by a 20% increase in the breeding threshold; e, 80% of mothers affected by a 50% increase in the breeding threshold; f, 80% of mothers affected by a 80% increase in the breeding threshold as presented in Table 4.3.

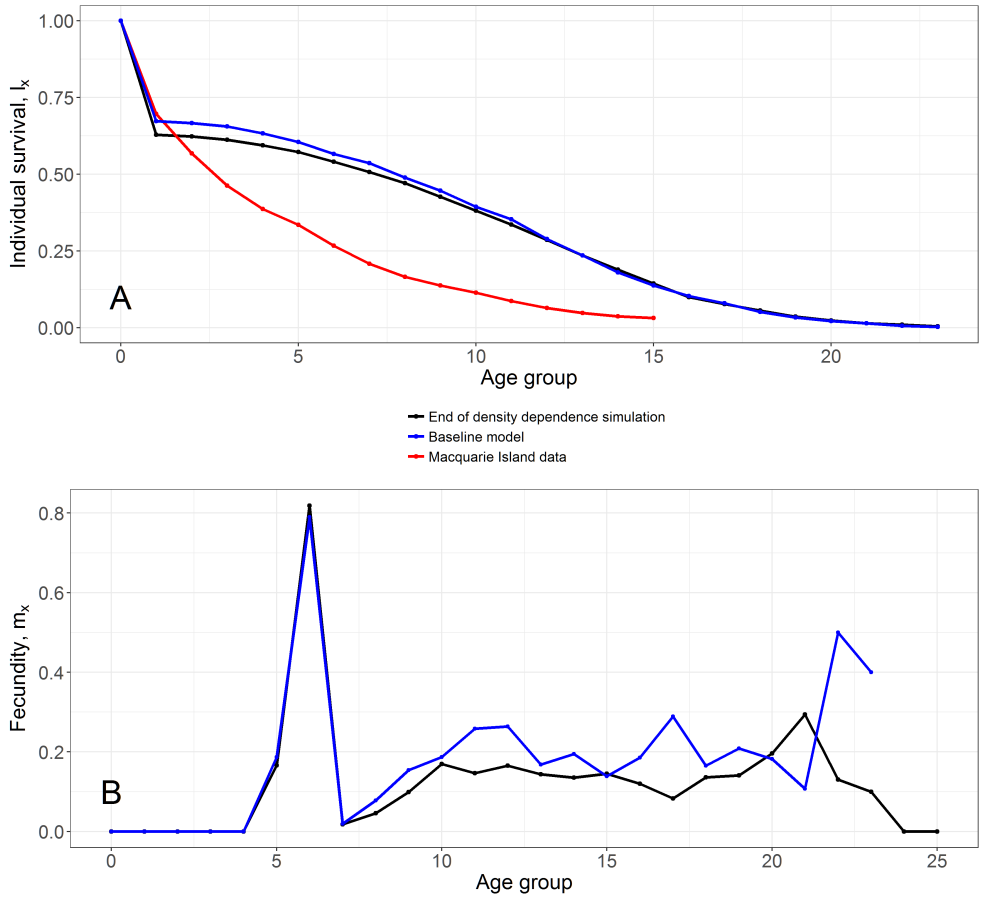

Figure A5. A) A comparison of the proportion of individuals surviving from one age group to the next l_x in the baseline model (blue), for a density dependence scenario (black) and Macquarie Island observations (red). B) Comparison of lifetime fecundity m_x for the baseline model (blue) and for a density dependence scenario (black). Full life data is presented in Tables 4.1, A3 and A14.

A5 Tables for Chapter 4: Using the DEB-IBM to test hypotheses on the potential drivers of the observed population decline in southern elephant seals at Macquarie Island

Appendix A5

Table A3. Emergent life history table for the baseline model as presented in Goedegebuure et al. (2018). Means (±standard deviation) from Monte Carlo simulations (n = 10 over 100 years). Results for lifespan of individuals exclude deaths of yearlings, and proportion of juveniles excludes counts of yearlings.

	Baseline data
Population size	1464±11
Percentage of juveniles in population	49.83±0.71%
Percentage of adults in population	39.51±0.74%
Pup survival	97.55±0.36%
Yearling survival	65.76±2.17%
Age at first reproduction (yr)	4.40±0.00
Generation time (yr)	9.49±0.03
Juvenile age (yr)	3.85±0.07
Min adult age (yr)	5.11±0.04
Adult age (yr)	10.74±0.06
Lifespan (yr)	11.73±0.08
Max lifespan (yr)	28.80±0.99
Fecundity	0.28±0.00
Max number of births per mum	8.9±1.10
Juvenile size (cm)	168±0.16
Adult size (cm)	188±0.31
Max size (cm)	193±0.59
Relative food availability for (age >360 d)	0.71±0.00

Appendix A5

Table A4. Life table for baseline model of Goedegebuure et al. (2018). Results are means of ten model runs. Headings of table following Krebs et al. (1989); Nelson (2017): d_x = Proportion of individuals of a cohort dying during the age interval X; q_x = Finite rate of mortality during the age interval X to X+1; p_x = Finite rate of survival during the age interval X to X+1; l_x = Proportion of individuals surviving at the start of age interval X; m_x = Mean fecundity of a cohort during the age interval X; $l_x m_x$ = Mean fecundity per age class.

	surv rate	surv prop	mort prop	mort rate	mean fec	mean fec per age group
Age group	p_x	l_x	d_x	q_x	m_x	$l_x m_x$
Birth	0.673	1.000		0.327	0.000	0.000
0-1	0.991	0.673	0.327	0.009	0.000	0.000
1-2	0.983	0.667	0.006	0.017	0.000	0.000
2-3	0.965	0.656	0.011	0.035	0.000	0.000
3-4	0.956	0.633	0.023	0.044	0.000	0.000
4-5	0.936	0.605	0.028	0.064	0.187	0.113
5-6	0.948	0.566	0.039	0.052	0.790	0.447
6-7	0.911	0.536	0.030	0.089	0.020	0.011
7-8	0.914	0.489	0.048	0.086	0.078	0.038
8-9	0.882	0.447	0.042	0.118	0.154	0.069
9-10	0.897	0.394	0.053	0.103	0.187	0.074
10-11	0.818	0.353	0.041	0.182	0.259	0.091
11-12	0.814	0.289	0.064	0.186	0.264	0.076
12-13	0.768	0.235	0.054	0.232	0.168	0.040
13-14	0.761	0.181	0.055	0.239	0.194	0.035
14-15	0.748	0.137	0.043	0.252	0.139	0.019
15-16	0.776	0.103	0.035	0.224	0.185	0.019
16-17	0.648	0.080	0.023	0.352	0.289	0.023
17-18	0.650	0.052	0.028	0.350	0.165	0.009
18-19	0.657	0.034	0.018	0.343	0.209	0.007
19-20	0.636	0.022	0.012	0.364	0.182	0.004
20-21	0.429	0.014	0.008	0.571	0.107	0.002
21-22	0.417	0.006	0.008	0.583	0.500	0.003

Appendix A5

Table A5. Life table for model population with implementation of Hypothesis 1 - Southern Annular Model events (SAM-like) simulation, at end of model's simulation. Headings of table as per Table A4, following Krebs et al. (1989); Nelson (2017).

	surv rate	surv prop	mort prop	mort rate	mean fec	mean fec per age group
Age group	p_x	l_x	d_x	q_x	m_x	$l_x m_x$
Birth	0.715	1.000		0.285	0.000	0.000
0-1	0.991	0.715	0.285	0.009	0.000	0.000
1-2	0.983	0.709	0.006	0.017	0.000	0.000
2-3	0.932	0.696	0.012	0.068	0.000	0.000
3-4	0.943	0.649	0.048	0.057	0.000	0.000
4-5	0.943	0.612	0.037	0.057	0.595	0.364
5-6	0.907	0.576	0.035	0.093	0.405	0.233
6-7	0.949	0.523	0.054	0.051	0.004	0.002
7-8	0.917	0.496	0.027	0.083	0.063	0.031
8-9	0.750	0.455	0.041	0.250	0.386	0.176
9-10	0.897	0.341	0.114	0.103	0.079	0.027
10-11	0.858	0.306	0.035	0.142	0.014	0.004
11-12	0.843	0.262	0.043	0.157	0.157	0.041
12-13	0.682	0.221	0.041	0.318	0.243	0.054
13-14	0.712	0.151	0.070	0.288	0.055	0.008
14-15	0.808	0.107	0.043	0.192	0.000	0.000
15-16	0.810	0.087	0.021	0.190	0.071	0.006
16-17	0.471	0.070	0.017	0.529	0.265	0.019
17-18	0.688	0.033	0.037	0.313	0.063	0.002
18-19	0.909	0.023	0.010	0.091	0.000	0.000
19-20	0.600	0.021	0.002	0.400	0.000	0.000
20-21	0.667	0.012	0.008	0.333	0.333	0.004
21-22	0.750	0.008	0.004	0.250	0.000	0.000
22-23	0.667	0.006	0.002	0.333	0.000	0.000

Appendix A5

Table A6. Life table for model population with implementation of Hypothesis 1 - El Niño Southern Oscillation (ENSO-like) simulation, at end of model's simulation. Headings of table as per Table A4, following Krebs et al. (1989); Nelson (2017).

	surv rate	surv prop	mort prop	mort rate	mean fec	mean fec per age group
Age group	p_x	l_x	d_x	q_x	m_x	$l_x m_x$
Birth	0.287	1.000		0.713	0.000	0.000
0-1	0.981	0.287	0.713	0.019	0.000	0.000
1-2	1.000	0.281	0.006	0.000	0.000	0.000
2-3	0.961	0.281	0.000	0.039	0.000	0.000
3-4	0.918	0.270	0.011	0.082	0.000	0.000
4-5	0.944	0.248	0.022	0.056	1.000	0.248
5-6	0.976	0.234	0.014	0.024	0.000	0.000
6-7	0.867	0.229	0.006	0.133	0.349	0.080
7-8	0.875	0.198	0.030	0.125	0.139	0.028
8-9	0.937	0.174	0.025	0.063	0.159	0.028
9-10	0.898	0.163	0.011	0.102	0.322	0.052
10-11	0.811	0.146	0.017	0.189	0.340	0.050
11-12	0.907	0.118	0.028	0.093	0.279	0.033
12-13	0.872	0.107	0.011	0.128	0.487	0.052
13-14	0.706	0.094	0.014	0.294	0.441	0.041
14-15	0.792	0.066	0.028	0.208	0.167	0.011
15-16	0.632	0.052	0.014	0.368	0.053	0.003
16-17	0.583	0.033	0.019	0.417	0.000	0.000
17-18	1.000	0.019	0.014	0.000	0.286	0.006
18-19	0.286	0.019	0.000	0.714	0.286	0.006

Table A7. Life table for model population with implementation of Hypothesis 2 - Reduction of yearling survival, at end of model's simulation. Headings of table as per Table A4, following Krebs et al. (1989); Nelson (2017).

	surv rate	surv prop	mort prop	mort rate	mean fec	mean fec per age group
Age group	p_x	l_x	d_x	q_x	m_x	$l_x m_x$
Birth	0.262	1.000		0.738	0.000	0.000
0-1	1.000	0.262	0.738	0.000	0.000	0.000
1-2	0.981	0.262	0.000	0.019	0.000	0.000
2-3	0.981	0.257	0.005	0.019	0.000	0.000
3-4	1.000	0.252	0.005	0.000	0.000	0.000
4-5	0.941	0.252	0.000	0.059	0.498	0.126
5-6	0.979	0.238	0.015	0.021	0.308	0.073
6-7	0.894	0.233	0.005	0.106	0.357	0.083
7-8	0.976	0.208	0.025	0.024	0.348	0.072
8-9	0.927	0.203	0.005	0.073	0.283	0.057
9-10	0.895	0.188	0.015	0.105	0.353	0.066
10-11	0.882	0.168	0.020	0.118	0.318	0.053
11-12	0.933	0.149	0.020	0.067	0.347	0.051
12-13	0.750	0.139	0.010	0.250	0.264	0.037
13-14	0.810	0.104	0.035	0.190	0.257	0.027
14-15	0.765	0.084	0.020	0.235	0.282	0.024
15-16	0.846	0.064	0.020	0.154	0.292	0.019
16-17	0.727	0.054	0.010	0.273	0.364	0.020
17-18	0.750	0.040	0.015	0.250	0.325	0.013
18-19	1.000	0.030	0.010	0.000	0.300	0.009
19-20	0.500	0.030	0.000	0.500	0.300	0.009
20-21	0.667	0.015	0.015	0.333	0.333	0.005

Table A8. Life table for model population with implementation of Hypothesis 3 - Reduction of the fecundity of mothers, 50% affected by 20% increase in reproductive threshold. Headings of table as per Table A4, following Krebs et al. (1989); Nelson (2017).

	surv rate	surv prop	mort prop	mort rate	mean fec	mean fec per age group
Age group	p_x	l_x	d_x	q_x	m_x	$l_x m_x$
Birth	0.616	1.000		0.384	0.000	0.000
0-1	0.981	0.616	0.384	0.019	0.000	0.000
1-2	0.955	0.605	0.012	0.045	0.000	0.000
2-3	0.966	0.578	0.027	0.034	0.000	0.000
3-4	0.972	0.558	0.019	0.028	0.000	0.000
4-5	0.936	0.543	0.016	0.064	0.210	0.114
5-6	0.931	0.508	0.035	0.069	0.438	0.222
6-7	0.943	0.473	0.035	0.057	0.151	0.071
7-8	0.878	0.446	0.027	0.122	0.101	0.045
8-9	0.871	0.391	0.054	0.129	0.198	0.078
9-10	0.932	0.341	0.050	0.068	0.241	0.082
10-11	0.817	0.318	0.023	0.183	0.212	0.067
11-12	0.866	0.260	0.058	0.134	0.194	0.050
12-13	0.845	0.225	0.035	0.155	0.155	0.035
13-14	0.755	0.190	0.035	0.245	0.184	0.035
14-15	0.838	0.143	0.047	0.162	0.189	0.027
15-16	0.839	0.120	0.023	0.161	0.181	0.022
16-17	0.769	0.101	0.019	0.231	0.162	0.016
17-18	0.550	0.078	0.023	0.450	0.150	0.012
18-19	0.636	0.043	0.035	0.364	0.200	0.009
19-20	0.714	0.027	0.016	0.286	0.143	0.004
20-21	0.400	0.019	0.008	0.600	0.160	0.003
21-22	0.500	0.008	0.012	0.500	0.500	0.004

Table A9. Life table for model population with implementation of Hypothesis 3 - Reduction of the fecundity of mothers, 50% affected by 50% increase in reproductive threshold. Headings of table as per Table A4, following Krebs et al. (1989); Nelson (2017).

	surv rate	surv prop	mort prop	mort rate	mean fec	mean fec per age group
Age group	p_x	l_x	d_x	q_x	m_x	$l_x m_x$
Birth	0.617	1.000		0.383	0.000	0.000
0-1	1.000	0.617	0.383	0.000	0.000	0.000
1-2	0.976	0.617	0.000	0.024	0.000	0.000
2-3	0.983	0.602	0.015	0.017	0.000	0.000
3-4	0.933	0.592	0.010	0.067	0.000	0.000
4-5	0.928	0.552	0.040	0.072	0.207	0.114
5-6	0.922	0.512	0.040	0.078	0.297	0.152
6-7	0.895	0.473	0.040	0.105	0.061	0.029
7-8	0.894	0.423	0.050	0.106	0.226	0.096
8-9	0.882	0.378	0.045	0.118	0.247	0.094
9-10	0.836	0.333	0.045	0.164	0.257	0.086
10-11	0.821	0.279	0.055	0.179	0.232	0.065
11-12	0.870	0.229	0.050	0.130	0.322	0.074
12-13	0.725	0.199	0.030	0.275	0.265	0.053
13-14	0.828	0.144	0.055	0.172	0.283	0.041
14-15	0.625	0.119	0.025	0.375	0.358	0.043
15-16	0.733	0.075	0.045	0.267	0.373	0.028
16-17	0.909	0.055	0.020	0.091	0.291	0.016
17-18	0.800	0.050	0.005	0.200	0.260	0.013
18-19	0.750	0.040	0.010	0.250	0.050	0.002
19-20	0.667	0.030	0.010	0.333	0.100	0.003
20-21	0.750	0.020	0.010	0.250	0.150	0.003
21-22	1.000	0.015	0.005	0.000	0.200	0.003

Appendix A5

Table A10. Life table for model population with implementation of Hypothesis 3 - Reduction of the fecundity of mothers, 50% affected by 80% increase in reproductive threshold. Headings of table as per Table A4, following Krebs et al. (1989); Nelson (2017).

	surv rate	surv prop	mort prop	mort rate	mean fec	mean fec per age group
Age group	p_x	l_x	d_x	q_x	m_x	$l_x m_x$
Birth	0.625	1.000		0.375	0.000	0.000
0-1	0.975	0.625	0.375	0.025	0.000	0.000
1-2	1.000	0.609	0.016	0.000	0.000	0.000
2-3	0.966	0.609	0.000	0.034	0.000	0.000
3-4	0.956	0.589	0.021	0.044	0.000	0.000
4-5	0.917	0.563	0.026	0.083	0.256	0.144
5-6	0.939	0.516	0.047	0.061	0.196	0.101
6-7	0.925	0.484	0.031	0.075	0.030	0.015
7-8	0.919	0.448	0.036	0.081	0.172	0.077
8-9	0.886	0.411	0.036	0.114	0.304	0.125
9-10	0.871	0.365	0.047	0.129	0.280	0.102
10-11	0.803	0.318	0.047	0.197	0.256	0.081
11-12	0.878	0.255	0.063	0.122	0.249	0.064
12-13	0.884	0.224	0.031	0.116	0.274	0.061
13-14	0.763	0.198	0.026	0.237	0.242	0.048
14-15	0.621	0.151	0.047	0.379	0.276	0.042
15-16	0.889	0.094	0.057	0.111	0.433	0.041
16-17	0.688	0.083	0.010	0.313	0.350	0.029
17-18	0.636	0.057	0.026	0.364	0.327	0.019
18-19	0.571	0.036	0.021	0.429	0.286	0.010
19-20	0.250	0.021	0.016	0.750	0.450	0.009

Table A11. Life table for model population with implementation of Hypothesis 3 - Reduction of the fecundity of mothers, 80% affected by 20% increase in reproductive threshold. Headings of table as per Table A4, following Krebs et al. (1989); Nelson (2017).

	surv rate	surv prop	mort prop	mort rate	mean fec	mean fec per age group
Age group	p_x	l_x	d_x	q_x	m_x	$l_x m_x$
Birth	0.565	1.000		0.435	0.000	0.000
0-1	0.979	0.565	0.435	0.021	0.000	0.000
1-2	0.989	0.553	0.012	0.011	0.000	0.000
2-3	0.989	0.547	0.006	0.011	0.000	0.000
3-4	0.967	0.541	0.006	0.033	0.000	0.000
4-5	0.910	0.524	0.018	0.090	0.126	0.066
5-6	0.926	0.476	0.047	0.074	0.496	0.236
6-7	0.960	0.441	0.035	0.040	0.227	0.100
7-8	0.889	0.424	0.018	0.111	0.175	0.074
8-9	0.859	0.376	0.047	0.141	0.228	0.086
9-10	0.855	0.324	0.053	0.145	0.327	0.106
10-11	0.809	0.276	0.047	0.191	0.306	0.085
11-12	0.816	0.224	0.053	0.184	0.358	0.080
12-13	0.839	0.182	0.041	0.161	0.290	0.053
13-14	0.769	0.153	0.029	0.231	0.331	0.051
14-15	0.850	0.118	0.035	0.150	0.260	0.031
15-16	0.706	0.100	0.018	0.294	0.294	0.029
16-17	0.583	0.071	0.029	0.417	0.333	0.024
17-18	0.429	0.041	0.029	0.571	0.371	0.015
18-19	1.000	0.018	0.024	0.000	0.600	0.011
19-20	0.667	0.018	0.000	0.333	0.333	0.006
20-21	0.500	0.012	0.006	0.500	0.300	0.004

Table A12. Life table for model population with implementation of Hypothesis 3 - Reduction of the fecundity of mothers, 80% affected by 50% increase in reproductive threshold. Headings of table as per Table A4, following Krebs et al. (1989); Nelson (2017).

	surv rate	surv prop	mort prop	mort rate	mean fec	mean fec per age group
Age group	p_x	l_x	d_x	q_x	m_x	$l_x m_x$
Birth	0.597	1.000		0.403	0.000	0.000
0-1	0.992	0.597	0.403	0.008	0.000	0.000
1-2	0.992	0.592	0.005	0.008	0.000	0.000
2-3	0.983	0.587	0.005	0.017	0.000	0.000
3-4	0.974	0.577	0.010	0.026	0.000	0.000
4-5	0.965	0.562	0.015	0.035	0.076	0.043
5-6	0.908	0.542	0.020	0.092	0.150	0.082
6-7	0.909	0.493	0.050	0.091	0.152	0.075
7-8	0.900	0.448	0.045	0.100	0.240	0.107
8-9	0.889	0.403	0.045	0.111	0.240	0.097
9-10	0.917	0.358	0.045	0.083	0.272	0.098
10-11	0.879	0.328	0.030	0.121	0.324	0.106
11-12	0.741	0.289	0.040	0.259	0.283	0.082
12-13	0.837	0.214	0.075	0.163	0.391	0.084
13-14	0.750	0.179	0.035	0.250	0.406	0.073
14-15	0.815	0.134	0.045	0.185	0.363	0.049
15-16	0.682	0.109	0.025	0.318	0.382	0.042
16-17	0.933	0.075	0.035	0.067	0.373	0.028
17-18	0.500	0.070	0.005	0.500	0.329	0.023
18-19	0.714	0.035	0.035	0.286	0.571	0.020
19-20	0.400	0.025	0.010	0.600	0.360	0.009
20-21	0.500	0.010	0.015	0.500	0.500	0.005

Appendix A5

Table A13. Life table for model population with implementation of Hypothesis 3 - Reduction of the fecundity of mothers, 80% affected by 80% increase in reproductive threshold. Headings of table as per Table A4, following Krebs et al. (1989); Nelson (2017).

	surv rate	surv prop	mort prop	mort rate	mean fec	mean fec per age group
Age group	p_x	l_x	d_x	q_x	m_x	$l_x m_x$
Birth	0.641	1.000		0.359	0.000	0.000
0-1	0.992	0.641	0.359	0.008	0.000	0.000
1-2	0.992	0.635	0.005	0.008	0.000	0.000
2-3	0.992	0.630	0.005	0.008	0.000	0.000
3-4	0.975	0.625	0.005	0.025	0.000	0.000
4-5	0.932	0.609	0.016	0.068	0.091	0.055
5-6	0.954	0.568	0.042	0.046	0.066	0.038
6-7	0.942	0.542	0.026	0.058	0.015	0.008
7-8	0.898	0.510	0.031	0.102	0.153	0.078
8-9	0.932	0.458	0.052	0.068	0.225	0.103
9-10	0.829	0.427	0.031	0.171	0.237	0.101
10-11	0.882	0.354	0.073	0.118	0.247	0.088
11-12	0.883	0.313	0.042	0.117	0.213	0.067
12-13	0.774	0.276	0.036	0.226	0.242	0.067
13-14	0.805	0.214	0.063	0.195	0.273	0.058
14-15	0.848	0.172	0.042	0.152	0.261	0.045
15-16	0.750	0.146	0.026	0.250	0.271	0.040
16-17	0.667	0.109	0.036	0.333	0.314	0.034
17-18	0.786	0.073	0.036	0.214	0.271	0.020
18-19	0.364	0.057	0.016	0.636	0.291	0.017
19-20	0.250	0.021	0.036	0.750	0.450	0.009

Table A14. Life table for model population with implementation of Hypothesis 4 - Density dependent population decline at end of simulation. Results are means of ten model runs. Headings of table as per Table A4, following Krebs et al. (1989); Nelson (2017).

Age group	surv rate p_x	surv prop l_x	mort prop d_x	mort rate q_x	mean fec m_x	mean fec per age group $l_x m_x$
Birth	0.628	1.000		0.372	0.000	0.000
0-1	0.993	0.628	0.372	0.007	0.000	0.000
1-2	0.981	0.624	0.005	0.019	0.000	0.000
2-3	0.971	0.612	0.012	0.029	0.000	0.000
3-4	0.964	0.594	0.018	0.036	0.000	0.000
4-5	0.945	0.573	0.021	0.055	0.166	0.095
5-6	0.938	0.541	0.032	0.062	0.818	0.443
6-7	0.928	0.507	0.034	0.072	0.018	0.009
7-8	0.906	0.471	0.037	0.094	0.046	0.022
8-9	0.894	0.426	0.044	0.106	0.099	0.042
9-10	0.881	0.381	0.045	0.119	0.169	0.065
10-11	0.852	0.336	0.045	0.148	0.146	0.049
11-12	0.821	0.286	0.050	0.179	0.166	0.047
12-13	0.805	0.235	0.051	0.195	0.144	0.034
13-14	0.761	0.189	0.046	0.239	0.135	0.026
14-15	0.694	0.144	0.045	0.306	0.145	0.021
15-16	0.769	0.100	0.044	0.231	0.120	0.012
16-17	0.733	0.077	0.023	0.267	0.083	0.006
17-18	0.644	0.056	0.021	0.356	0.136	0.008
18-19	0.659	0.036	0.020	0.341	0.141	0.005
19-20	0.607	0.024	0.012	0.393	0.196	0.005
20-21	0.676	0.015	0.009	0.324	0.294	0.004
21-22	0.435	0.010	0.005	0.565	0.130	0.001
22-23	0.500	0.004	0.006	0.500	0.100	0.000

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